# Foregut anatomy, feeding mechanisms, relationships and classification of the Conoidea (= Toxoglossa) (Gastropoda)

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## CONTENTS

SYNOPSIS. A survey of the anterior alimentary system of species from all the higher taxa of the highly diverse gastropod superfamily Conoidea (including the Turridae, Terebridae, and Conidae) has revealed a great variety of foregut structure. A series of anatomical characters of the rhynchodeum, proboscis, buccal mass, radular apparatus and foregut glands has been defined and their distribution established amongst the various conoidean families and sub-families. Twelve major types of foregut structure were recognised, which ranged from gastropods with a full set of foregut organs and glands to others in which most of the structures including the radula, venom gland and proboscis are absent. A set of these anatomical characters together with a few shell characters were used in a cladistic analysis attempting to determine relationships amongst the conoidean higher taxa. A classification incorporating the new anatomical data and based partly upon the phylogenetic analysis recognises 6 families and 13 subfamilies of Conoidea. New data suggest that the Pervicaciinae and Terebrinae share a common ancestor and there is little evidence to justify familial separation of the Coninae. Some major foregut structures seem to have evolved independently in different clades. Thus, hollow 'hypodermic' radular teeth have been derived independently in a least five clades; the radular caecum and rhynchodeal introvert have evolved independently in two clades. Several clades also show loss of major foregut structures such as the proboscis, venom gland and radular apparatus. Finally, the 378 genera of Recent 'Turridae' are placed into the higher taxa recognised in the proposed classification.

# INTRODUCTION

The prosobranch gastropod superfamily Conoidea (=Toxoglossa), which includes the families Turridae, Conidae, Pervicaciidae and Terebridae, is extremely diverse, with as many as 679 genera and 10,000 living and fossil species claimed for the Turridae alone (Bouchet, 1990) and *Conus* with around 500 living species, is considered to be the most diverse genus of marine animal (Kohn, 1990). Current classifications of taxa within the Conoidea are based almost entirely upon shell characters, or upon a combination of shell and radular characters (Turridae–Powell, 1966; McLean 1971; Kilburn, 1983, 1985, 1986, 1988; Terebridae–Bratcher & Cernohorsky, 1987). The Turridae are the most morphologically disparate of the four families with seventeen subfamilies in current use. However, most of these subfamilies are rather poorly defined. Despite the biological interest in the venom apparatus of the group, little is known of the relationships of the Conoidea to other gastropods, of relationships between the families of the Conoidea or of relationships within the constituent families.

The Conoidea are considered to be monophyletic, because the families share the common apomorphy of a venom apparatus con-sisting of the venom gland and muscular bulb. This is thought to have been lost in some taxa, such as some highly-derived members of the Daphnellinae and Terebridae (Kantor & Sysoev 1989; Taylor, 1990) and all Strictispirinae.

Compared with the number of living species and the attention paid to the description of shells, particularly of Conidae, there have been very few anatomical studies of Conoidea. However, recently, a much wider range of species from the Turridae, Terebridae and Pervicaciidae (Sysoev & Kantor 1987, 1988, 1989; Kantor & Sysoev, 1989; Miller, 1989, 1990; Kantor, 1990; Taylor, 1990) have been investigated anatomically. These studies illustrate the great variety of foregut anatomy, particularly within the Turridae and Terebridae. By comparison, the Conidae appear to have a relatively uniform foregut anatomy (Marsh, 1971; Miller, 1989), although they have been surprisingly little studied.

Until recently, attempts to use anatomical characters in determining relationships amongst conoideans were constrained either by the limited range of taxa that had been studied or by the small number of characters used. For example, an evolutionary scenario for the Conoidea based upon characters of foregut anatomy was proposed by Sheridan et al. (1973), but species were studied from only three out of the seventeen turrid subfamilies. Additionally, Shimek & Kohn (1981) used only radular characters to produce a cladistic analysis of a wider range turrid taxa.

Another problem in comparing the different taxa studied within the Conoidea, is that the nomenclature for the different anatomical structures is inconsistent and very confused. This has hampered the recognition of homologous structures that may be shared between the different taxa.

In this paper we attempt a comparative review of the anatomy and functional morphology of the conoidean foregut. We have attempted to examine species from all the currently-recognised subfamilies of Turridae, many species of Terebridae, Pervicaciidae and a few species of Conus. Additionally, we have incorporated previously published studies into our review and attempted to standardize the nomenclature of the anatomical structures.

The overall objectives of the study are, firstly, to evalu-ate the use of characters of foregut anatomy in determining relationships among the Conoidea and secondly, to propose a new classification of conoidean higher taxa which incorporates these anatomical characters. Foregut anatomy was chosen as the focus for this study, because a few previous studies (Sheridan et al. 1973; Kantor, 1990) had drawn attention to the diversity and complexity of the digestive system. As far as is known, other organ systems are similar to other neogastropods.

## MATERIAL AND METHODS

The material on which this study is based consists mainly of longitudinal serial sections of the foreguts of a wide range of gastropods from all of the currently recognised subfamilies of Turridae, many Terebridae and Pervicaciidae and a few species of Conidae (Table 1). Dissections were also made of most of these species. Also indicated in Table 1 are species for which we have used previously published anatomical

descriptions in our analysis. Additionally, radular preparations were made from a range of other species.

Critical-point dried preparations for scanning electron microscopy were made of some anatomical structures and some small species (methods in Taylor & Miller, 1989). Radula preparations for both light and scanning microscopy were made by standard methods.

## FOREGUT ANATOMY

A generalized diagram of the conoidean foregut (Fig. 1) shows the relative positions of the major structures.
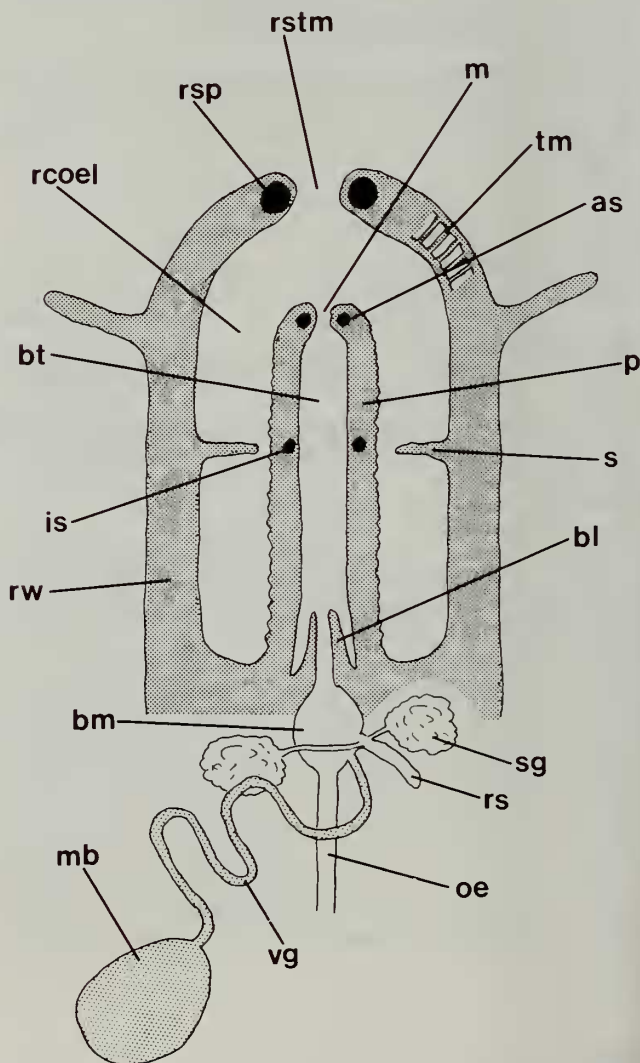


Fig. 1   Composite diagram of the foregut of a hypothetical conoidean gastropod showing the location of the major structures discussed in the text. No single gastropod possesses all these features. Abbreviations: as, anterior sphincter of buccal tube; bl, buccal lips; bm, buccal mass; bt, buccal tube; is, intermediate sphincter of buccal tube; m, mouth; mb; muscular bulb; oe, oesophagus; p, proboscis; rcoel, rhynchocoel; rs, radular sac; rsp, rhynchostomal sphincter; rstm, rhynchostome; rw, rhynchodeal wall; s, septum; sg, salivary gland; tm, transverse muscles of rhynchodeal wall (shown in part only); vg, venom gland.

**Table 1.** List of species examined in this study. The classification in the list is traditional and follows Powell (1966), McLean (1971) and Kilburn (1983–89). A new classification is given at the end of this paper. The prefix 'a' denotes species that were studied anatomically and the prefix 'r' denotes species for which only the radula was examined. In most cases, animals were both dissected and serial sections made of the anterior alimentary systems.

**Pseudomelatominae**
a*Pseudomelatoma penicillata* (Carpenter, 1864). Punta San Bartoleme, Mexico.
a*Hormospira maculosa* (Sowerby, 1834). Sonora, Mexico

**Drilliinae**
a*Clavus unizonalis* (Lamarck, 1822). Lizard I., Queensland, Australia.
a*Clavus* sp. (undescribed species). Guam.
a*Splendrillia chathamensis* Sysoev & Kantor, 1989. Chatham Rise, South Pacific.
r*Drillia cydia* (Bartsch, 1943). British Virgin Islands.
r*Drillia rosacea* (Reeve, 1845). West Africa.
r*Imaclava unimaculata* (Sowerby, 1834). Baja California, Mexico.
r*Spirotropis monterosatoi* (Locard, 1897). East Atlantic.
r*Crassopleura maravignae* (Bivona, 1838). Naples, Italy.

**Clavatulinae**
a*Toxoclionella tumida* (Sowerby, 1870). South Africa.
a*Clionella sinuata* (Born, 1778). Oudekraal, South Africa.
a*Clavatula caerulea* (Weinkauff, 1875). Sierra Leone, West Africa.
a*Clavatula muricata (Lamarck, 1822).* Dakar, Senegal.

**Turrinae**
r*Lophiotoma acuta* (Perry, 1811). Lizard I., Queensland, Australia.
a*Gemmula deshayesi* (Doumet, 1839). Hong Kong.
r*Gemmula kieneri* (Doumet, 1840). Hong Kong.
a*Lophiotoma leucotropis* (Adams & Reeve, 1850). Hong Kong.
a*Polystira albida* (Perry, 1811). Caribbean. Data from Leviten (1970).

**Cochlespirinae**
a*Turricula javana* (Linnaeus, 1767). Hong Kong.
a*Turricula nelliae spurius* (Hedley, 1922). Hong Kong.
a*Aforia abyssalis* Sysoev & Kantor, 1987. North-East Pacific.
a*Aforia lepta* (Watson, 1881). South Pacific, nr New Zealand.
a*Aforia inoperculata* Sysoev & Kantor, 1988. North-East Pacific.
a*Irenosyrinx hypomela* (Dall, 1889). East Atlantic.
a*Antiplanes sanctiioannis* (Smith, 1875). Okhotsk Sea.
r*Antiplanes vinosa* (Dall, 1874). Sakhalin Bay, Okhotsk Sea.

**Crassispirinae**
r*Austrodrillia angasi* (Crosse, 1863). Sydney, Australia.
a*Funa latisinuata* (Smith, 1877). Hong Kong.
a*Inquisitor* spp. Indian Ocean.
a*Vexitomina garrardi* (Laseron, 1954). Sydney, Australia.
r*Ptychobela griffithi* (Gray, 1834). Karachi.

**Strictispirinae**
a*Strictispira paxillus* (Reeve, 1845). British Virgin Islands.
r*Strictispira stillmani* Shasky, 1971. Panama.
r*Cleospira ochsneri* (Hertlein & Strong, 1849). Galapagos Islands.

**Zonulispirinae**
a*Pilsbryspira nympha* (Pilsbry & Lowe, 1932). Sonora, Mexico.

**Borsoniinae including Mitrolumninae** (fide Kilburn, 1986)
a*Lovellona atramentosa* (Reeve, 1849). Guam.
a*Anarithma metula* (Hinds, 1843). Indian Ocean.
a*Borsonia ochraea* Thiele, 1925. Indian Ocean, nr Zanzibar 740m.
a*Micanthapex parengonius* (Dell, 1956). South Pacific, nr New Zealand.
a*Tomopleura reevei* (C.B. Adams, 1850). Indian Ocean.
a*Suavodrillia kennicotti* (Dall, 1871). Japan Sea.
a*Tropidoturris anaglypta* Kilburn 1986. Southern Indian Ocean.
a*Tropidoturris fossata notialis* Kilburn, 1986. South Africa.
a*Ophiodermella inermis* (Hinds, 1843). Bremerton, Washington.
a*Ophiodermella ogurana* (Yokoyama, 1922). Japan Sea.

**Clathurellinae**
a*Glyphostoma candida* (Hinds, 1843). Sonora, Mexico.

**Mangeliinae**
a*Mangelia brachystoma* (Philippi, 1844). Galway, Ireland.
a*Mangelia nebula* (Montagu, 1803). Galway, Ireland. Also data from Sheridan *et al.* (1973) & Delaunois & Sheridan (1989).
a*Mangelia powisiana* (Dautzenberg, 1887). Plymouth, England.
a*Eucithara stromboides* (Reeve, 1846). Guam.
a*Hemilienardia malleti* (Recluz, 1852). Guam.
a*Paramontana* cf. *rufozonata* (Angas, 1877). Rottnest I., Western Australia.

**Oenopotinae**
a*Oenopota levidensis* (Dall, 1919). Washington. Data from Shimek (1975)
r*Propebela rugulata* (Moller, 1866). White Sea.

**Daphnellinae**
a*Comarmondia gracilis* (Montagu, 1803). Brittany, France. Data from Sheridan *et al.* (1973)
a*Daphnella reeveana* (Deshayes, 1863). Guam.
a*Gymnobela emertoni* (Verrill & Smith, 1884). Eastern Atlantic Ocean.
a*Teretiopsis levicarinatus* Kantor & Sysoev, 1989. Eastern Atlantic Ocean.
a*Abyssobela atoxica* Kantor & Sysoev, 1986. Northern Pacific Ocean.
a*Gymnobela latistriata* Kantor & Sysoev, 1986. Northern Pacific Ocean.
a*Gymnobela oculifera* Kantor & Sysoev, 1986. Northern Pacific Ocean.
a*Pontiothauma abyssicola* Smith, 1895. Indian Ocean. Data from Pacc (1901).
a*Pontiothauma mirabile* Smith, 1895. Indian Ocean. Data from Pace (1901)

**Conorbinae**
a*Benthofascis biconica (Hedley, 1903).* Sydney, Australia.
a*Genota mitraeformis* (Woods, 1828). West Africa.
a*Genota nicklesi* Knudsen, 1952. West Africa.

**Thatcheriinae**
a*Thatcheria mirabilis* Angas, 1877. North Western Australia.

**Taraniinae**
a*Taranis moerchi* (Malm, 1861). Sweden.

**Conidae**
a*Conus flavidus* Lamarck, 1810. Queensland, Australia, Data from Marsh (1971)
a*Conus ventricosus* Gmelin, 1791. Tunisia.

**Pervicaciidae**
a*Pervicacia capensis* (Smith, 1873). South Africa.
a*Pervicacia kieneri* (Deshayes, 1859) Albany, Western Australia.
a*Pervicacia tristis* (Deshayes, 1859). New Zealand.
a*Duplicaria colorata* Bratcher, 1988. Western Australia.
a*Duplicaria duplicata* (Linnaeus, 1758). Kenya.
a*Duplicaria spectabilis* (Hinds, 1844). Hong Kong.
a'*Terebra*' *nassoides* Hinds, 1844. Oman.

**Terebridae**
a*Hastula aciculina* (Lamarck, 1822). Ghana.
a*Hastula bacillus* (Deshayes, 1859). Phuket, Thailand.
a*Terebra affinis* Gray, 1834. Guam.
a*Terebra babylonia* Lamarck, 1822. Guam.
a*Terebra gouldi* Deshayes, 1857. Hawaii.
a*Terebra maculata* Linnaeus, 1758. Guam.
a*Terebra subulata* Linnaeus, 1767. Maldives.

## Characters of the rhynchocoel

In all toxoglossans there is a permanent cavity in the anterior part of the body called the rhynchodeal cavity or rhynchocoel (Fig. 1). It contains the proboscis and is maintained even when the proboscis is extended. The rhynchodeal cavity opens to the exterior via the rhynchostome, which is situated at the ventral margin of the head. The walls of the rhynchocoel (rhynchodeum) are usually thick and muscular.

### Rhynchostomal sphincter

This an annular, muscular sphincter which encircles the mouth of the rhynchocoel (Fig. 1). It is present in most species of Turridae, Terebridae, Pervicaciidae and Conidae, but absent in the turrids *Clavatula diadema* and *Tomopleura violacea* and the pervicaciids *Pervicacia tristis*, '*Terebra*' *nassoides*, and '*T.*' *capen-sis*. In these latter pervicaciids and some turrids without a prominent sphincter, for example *Tomopleura*, the anterior part of the rhynchodeum is very muscular.

### Position of rhynchostomal sphincter

In the normal condition, the sphincter is usually situated around the rhynchostome, but in some turrids (for example in *Glyphostoma*, *Borsonia*, *Lophiotoma*, *Pontiothauma* and *Thatcheria*) it is situated more posteriorly. In *Ophiodermella inermis* (but not *O. ogurana*) and *Suavodrillia kennicotti* the moderately large, posteriorly situated, rhynchostomal sphincter is probably able to evert, forming a sort of 'rhynchostomal introvert' but situated in the middle part of the rhynchocoel (Fig. 2). The ability to evert is indicated by the presence of a well-developed layer of longitudinal muscles underlying the epithelium and by the existence of free space between the sphincter and the longitudinal muscle layers. This structure may demonstrate the possible origin of the true rhynchodeal introvert (see below) or alternatively be an autapomorphy for the species.

### Rostrum

In the some fish-feeding species of *Conus*, the anterior part of the rhynchocoel is elastic and can be greatly extended to accomodate large food items during preliminary digestion. This extensible feature, known as the rostrum, cannot be inverted into the rhynchocoel.

### Rhynchodeal introvert (= labial tube or pseudoproboscis)

In this structure, the rhynchostomal lips are mobile and can be retracted into the rhynchocoel by infolding, or extended as a tube (Figs 3 & 4). The introvert is found in nearly all the species which we and others have studied from the turrid sub-family Daphnellinae, e.g. *Philbertia linearis*, *P. leufroyi*, *P. gracilis*, *Cenodagreutes*, *Daphnella reeveana* (Smith, 1967; Sheridan *et al.*, 1973; unpublished observations), in *Hemilienardia malleti* (Mangeliinae) and in all Terebridae and Pervicaciidae (Miller, 1975, 1980; Taylor, 1990). We have not seen an introvert in any other subfamily of Turridae (except perhaps for *Ophiodermella*, see above), or in the Conidae. In species of Daphnellinae the introvert is fairly short, but in some terebrids, for example *Terebra maculata*, the introvert
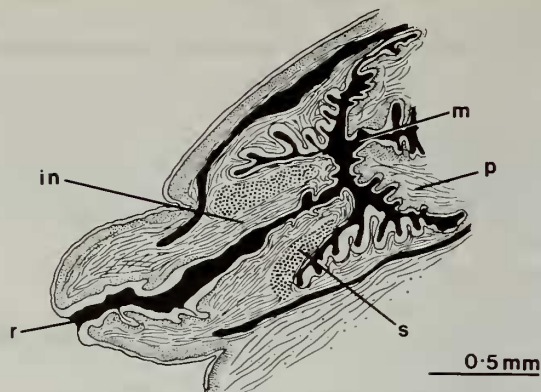


**Fig. 2** *Ophiodermella inermis*; longitudinal section of the anterior rhynchodaeum showing the posteriorly-situated, rhynchostomal sphincter located on an introvert-like structure. Abbreviations: in, introvert; m, mouth; p, proboscis; r, rhynchostome; s, sphincter.



**Fig. 3** *Hemilienardia malleti*; extended rhynchodeal introvert, forming a pseudoproboscis in a relaxed, critical-point dried specimen. Scale bar = 100 μm.

is very long, and when retracted, lies coiled in the rhynchocoel (Miller, 1970).

In those animals possessing a rhynchodeal introvert, the outer and inner walls are joined by radial muscles (Fig. 5). In Turridae, the possession of an introvert is associated with a reduction in size or complete loss of the proboscis. However, within the Terebridae, even those species with a well-developed proboscis possess an introvert.

### Epithelium of the rhynchodeum

In some Turridae, there is a distinct division in the character of the epithelium lining the inner wall of the rhynchocoel. In the anterior part of the cavity the epithelial cells are high and
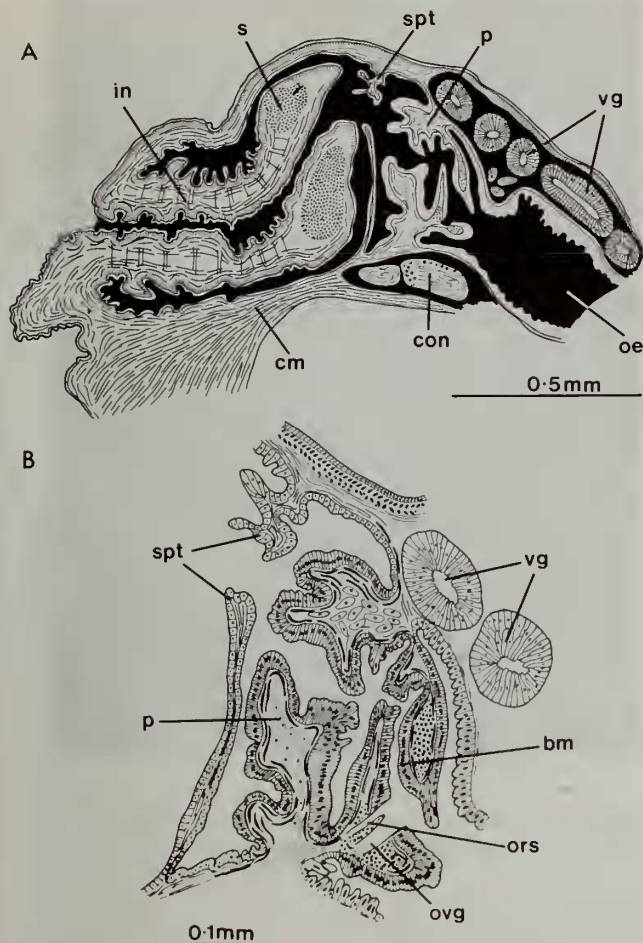
**Fig. 4**  *Daphnella reeveana*; A, longitudinal section through the foregut; B, Enlargement of the mouth area showing the short proboscis lying behind the septum. Abbreviations: bm, buccal mass; cm, columellar muscle; con, circum-oral nerve ring; in, rhynchodeal introvert; oe, oesophagus; ors, opening of radular sac; ovg, opening of venom gland; p, proboscis; s, rhynchostomal sphincter; spt, septum; vg, venom gland.

glandular (Fig. 6C), but in the posterior half the epithelium is low, cuticularized and similar in morphology to that of the outer surface of the proboscis. This feature indicates that the posterior part of the rhynchodeum can be extended outwards when the proboscis is protruded through the rhynchostome. We have observed this condition of the rhynchocoel epithelium in *Clavatula*, and *Clionella* (Clavatulinae), *Vexitomina* (Crassispirinae), *Turricula nelliae spurius* (Cochlespirinae), *Pilsbryspira nympha* (Zonulispirinae). and *Anarithma metula* (Borsoniinae).

In 'lower' turrids, excepting *Vexitomina*, this feature seems to associated with those species in which the buccal mass lies in a distal position within the proboscis (see below). Its presence may be connected with the mechanism by which the buccal mass is everted from the proboscis tip.

### Septum in rhynchodeum

A thin, slightly muscular septum, pierced by a circular orifice, and dividing the rhynchodeal cavity into two parts is known in *Daphnella reeveana* (Fig. 4), *Philbertia purpurea* (Sheridan *et al.*, 1973) and *Terebra subulata* (Taylor, 1990). The probos-

cis, when withdrawn, lies behind the septum, with the retracted introvert lying to the anterior. A probably homologous septum is also found at the extreme posterior and ventral end of the rhynchocoel in *Thatcheria* and *Pontiothauma* (Pace, 1901). A thin septum is also found in the posterior part of the rhynchocoel in *Pervicacia tristis* (not reported by Rudman (1969)) and in *Duplicaria kieneri* (Taylor, unpublished).

The function of the septum is unknown, but it appears better developed in species with a long proboscis and where the proboscis withdraws behind the septum.

### Accessory proboscis structure

This is an extensible muscular structure which arises from the left hand wall of the rhynchocoel. It has been found only a few species of Terebridae and Pervicaciidae. It is long and branched in *Hastula bacillus* (Taylor & Miller, 1990), shorter and club-like in *Terebra affinis* (Miller, 1971), '*Hastula*' *colorata* and *D. kieneri* and a curved, club-shape in *Terebra imitatrix* (Auffenberg & Lee, 1988). In *H. bacillus* the accessory proboscis is covered in possible chemosensory structures (Taylor & Miller (1990).

### Snout gland

This is a subspherical gland which opens into the right-hand posterior end of the rhynchocoel in a number of *Conus* species (Marsh, 1971). The gland consists of folded glandular epithelium (Fig. 7) and is surrounded by a muscular sheath of circular muscles. From histochemical tests, Marsh (1971) concluded that the gland secretes mucus. The gland has been reported in 18 species of *Conus*, all but one of which are known to be vermivorous (Marsh, 1971).

## The proboscis and its structures

An extensible proboscis arising from the posterior of the rhynchocoel is present in the Drilliinae (formerly Clavinae; ICZN decision pending on further name change to Clavusinae) and all the radulate turrids examined, excepting *Gymnobela emertoni*, where the radula is vestigial. A proboscis is present in all species of *Conus*, in *Hastula*, and in other radulate Terebridae, such as *T. subulata*, and *T. babylonia* (Taylor, 1990). The distal opening to the proboscis forms the true mouth as in all probosciferous gastropods. Shimek (1975) referred to the opening of the buccal cavity as being the true mouth.

A proboscis is absent in the radula-less Turridae such as *Teretiopsis*, *Taranis* (Kantor & Sysoev, 1989), *Philbertia leufroyi boothi*, *P. linearis* (Smith, 1967, Sheridan *et al.*, 1973) and the radulate *Gymnobela emertoni*. A proboscis is also absent in species of *Duplicaria* and *Pervicacia*, which are radulate forms of the Pervicaciidae (Taylor, 1990), and in the many species of Terebridae which lack a radula, such as *Terebra maculata*, *T. gouldi*, *T. dimidiata*, and *T. affinis* (Miller, 1970, 1975; Taylor, 1990).

In *Duplicaria spectabilis* and *Gymnobela emertoni* we have observed a low cylinder of muscular tissue surrounding the opening to the buccal cavity (Fig. 8) (Taylor (1990, Fig.2). We think that this may represent the remnant of a much reduced proboscis. A similar reduced structure found in *Cenodagreutes* spp. and *Philbertia linearis*, was described by Smith (1976) as the muscular sheath.
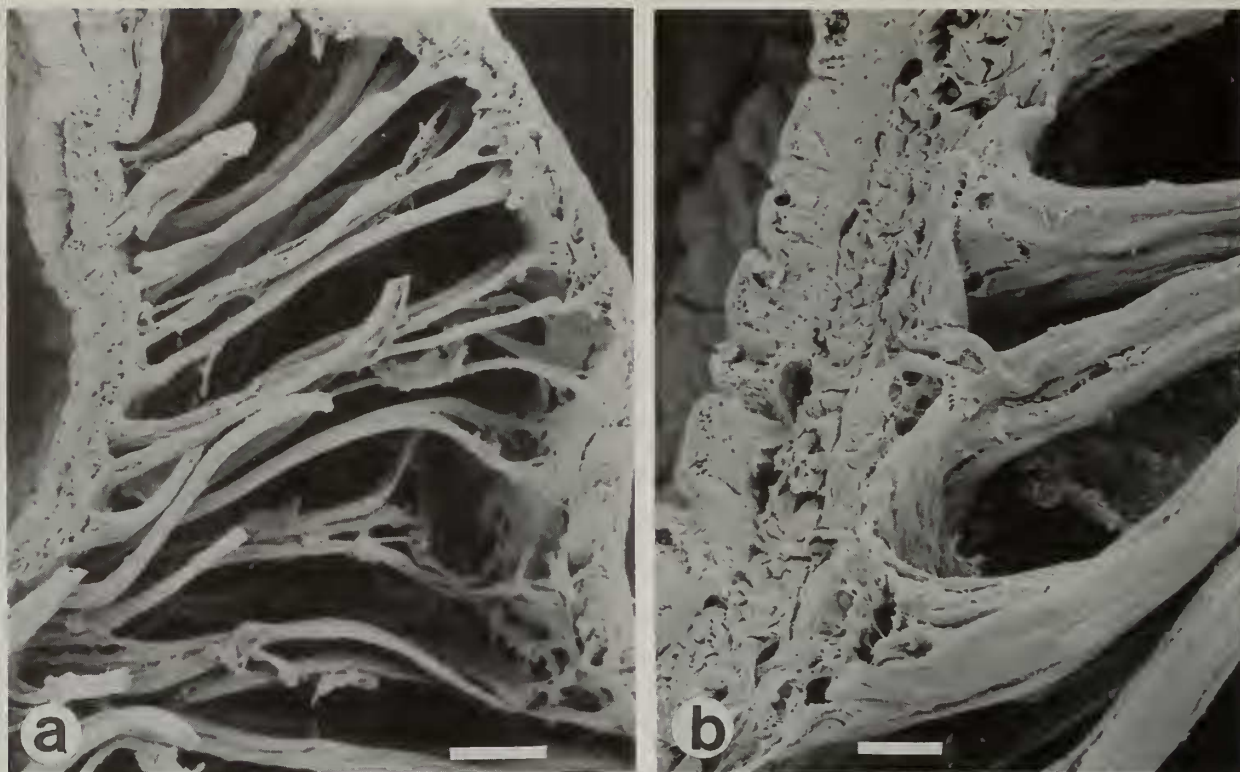
Fig. 5 *Duplicaria spectabilis*; relaxed, critical-point dried specimen. A, Section of the rhynchodeal wall showing the transverse muscles joining the inner and outer walls. Scale bar = 100 µm. B, Detail of junction of transverse muscles joining the inner wall of the rhynchodaeum. Scale bar = 20 µm.

## Buccal tube

The buccal tube is that portion of the alimentary canal lying between the buccal cavity and the true mouth, which is situated at the distal end of the proboscis. The buccal tube is present in all toxoglossans with a proboscis and is absent only in those species where that organ is lost. It is very short in *Strictispira paxillus* where the buccal mass lies at the extreme anterior end of the proboscis.

In the Mangeliinae the epithelium of the buccal tube is very thin (Fig. 9), but much thicker in species of other subfami-lies such as the Drilliinae and Clavatulinae (Fig. 6). Shimek (1975) refered to the buccal lips (see below) as the buccal tube, and he called the true buccal tube, the inner proboscis wall.

## Buccal tube sphincters

In most toxoglossans, one or more annular sphincters may be found in various positions within the proboscis.

### a) Distal sphincter(s)
In most species with a proboscis, there is a distal sphincter around the true mouth. Frequently, there is a second sphinc-ter also near the proboscis tip, but located just to the posterior of the first (Fig. 6). In 'lower' turrids such as the Drilliinae Cochlespirinae and Clavatulinae, the sphincter(s) grip the solid, radular teeth whilst they are held at the proboscis tip (Sysoev & Kantor, 1989; Kantor & Taylor, 1991).

### b) Intermediate sphincter
A small muscular sphincter, situated about half way along the length of the proboscis is found in *Splendrillia* (Kantor & Sysoev, 1989, fig. 3c). Species of *Conus* also have a sphincter situated some distance posterior to the proboscis tip (Greene & Kohn, 1989) which we classify as an intermediate sphinc-ter.

### c) Basal sphincter
A sphincter located near the base of the proboscis has been described for *Mangelia nebula* (Sheridan *et al.*, 1973). Recently, Delaunois & Sheridan (1989) have illustrated a section through the buccal area of *M. nebula*, showing a single radular tooth held in the buccal tube. The tooth is gripped at the anterior end by the buccal tube introvert (see below), and the posterior end by the basal sphincter (Fig. 9).

## Buccal tube introvert

This is a muscular, flap-like structure found towards the distal end of the buccal tube of *Mangelia nebula* (Fig. 9) and called a valve (valvule) by Sheridan *et al.* (1973). *Eucithara strom-boides* has a longer, but apparently homologous structure (Fig. 10). Delaunois & Sheridan (1989) showed that one of the functions of this structure is to grip the radular tooth in the buccal tube, but in *Eucithara* where the structure is very long (Fig.10), it may possibly be used to transport teeth to the proboscis tip.
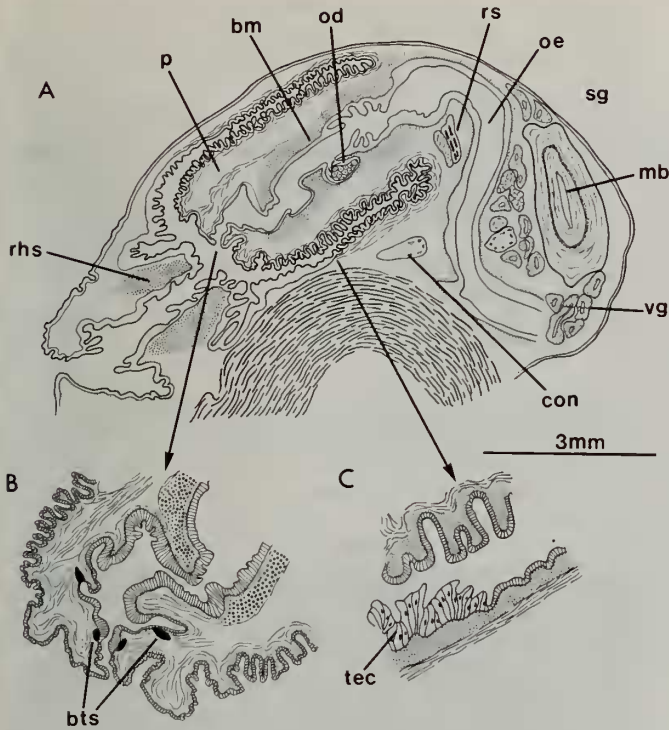
Fig. 6 *Clionella sinuata*; A, longitudinal section through the foregut; B, section of tip of proboscis showing sphincters; C, section of portion of the inner wall of the rhynchodeum, showing the differentiation in epithelium from that similar to the proboscis wall, to that typical of the lining of the rhynchocoel.
Abbreviations: bm, buccal mass; bts, buccal tube sphincters; con, circum-oral nerve ring; mb, muscular bulb; od, odontophore; oe, oesophagus; p, proboscis; rhs, rhynchostomal sphincter; rs, radular sac; sg, salivary gland; tec, tall epithelial cells; vg, venom gland.

## Sac-like enlargement of buccal tube

One other character associated with the gripping of marginal teeth at the proboscis tip, is the presence of a sac-like en-largement of the anterior or middle parts of the buccal tube. It is found in different 'lower' turrids (Kantor & Taylor, 1991) as well as *Mangelia nebula* (Sheridan *et al.*, 1973) and Conidae (*Conus catus* (Greene & Kohn, 1989) and *C. ventricosus*). Usually, the epithelium lining the enlargement is formed of much taller cells than in the rest of the buccal tube. These cells tightly surround the single radular teeth whilst they are being held at the proboscis tip and may afford a better grip. In *Splendrillia chathamensis*, Sysoev & Kantor (1989) found the base of tooth adhering to a pad of epithelial cells.

## Protrusive lips of proboscis/ buccal tube

In a few species, the inner lining of the outer lips of the proboscis can be protruded. For example, in *Turricula nelliae spurius*, the lips (Fig. 11) are densely covered by paddle or discocilia, which according to Haszprunar (1985) may indicate the presence of chemosensory cells. Similar protrusible lips are also found in *Lophiotoma leucotropis* and probably in *Aforia aulaca alaskana* (Sysoev & Kantor, 1987).

In relaxed specimens of *Mangelia powisiana*, a sac consisting of a single layer of cells is protruded from the proboscis
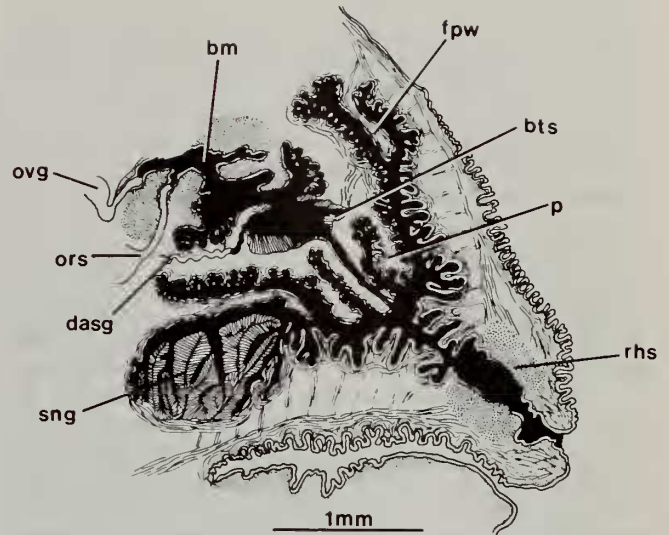


Fig. 7 *Conus ventricosus*; longitudinal section of the foregut showing the proboscis retracted into the rhynchodeum. Abbreviations: bm, buccal mass; bts, buccal tube sphincter; dasg, duct of accessory salivary gland; fpw, fold of proboscis wall; ors, opening of radular sac; ovg, opening of venom gland; p, proboscis; rhs, rhynchostomal sphincter; sng, snout gland.
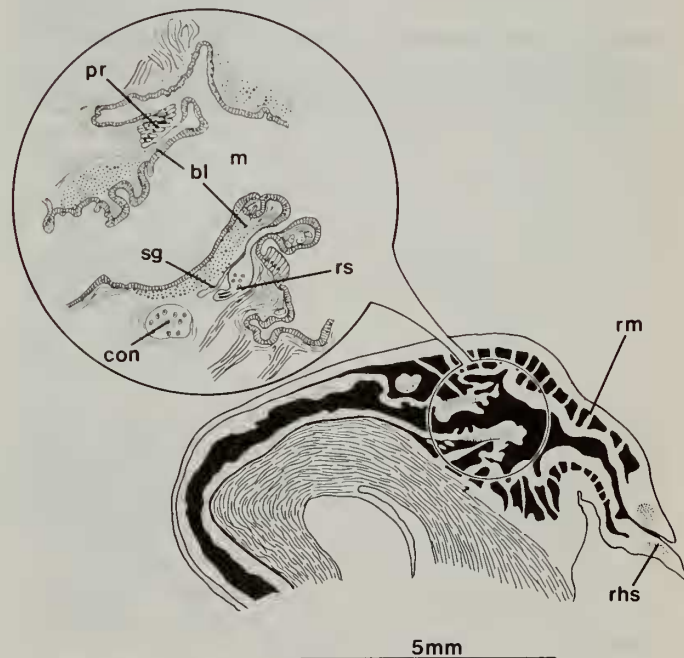


Fig. 8 *Gymnobela emertoni*; longitudinal section of the foregut showing, the remnants of the proboscis, buccal lips and vestigial radular sac. Abbreviations: bl, buccal lips; con, circum-oral nerve ring; m, mouth; pr, reduced proboscis; rhs, rhynchostomal sphincter; rm, radial muscles in rhynchodeal wall; rs, radular sac; sg, salivary gland.

tip (Fig. 12). This sac is covered in granule-like structures which are formed from single cells with large rounded nuclei. The distinctive epithelial cells seen at the proboscis tip of *Mangelia nebula* by Sheridan *et al.* (1973) may be the same structure but in a more contracted position. The function of this sac structure is not known.

## Position of the buccal mass

Three conditions are known in the Conoidea;

a)   Buccal mass situated at the base of the proboscis (Fig. 1)
For three reasons we consider this condition to be the primitive state within the Conoidea. Firstly, a basal buccal mass is found in species of the subfamily Drilliinae, which with five teeth in each radula row, are considered to possess the least-derived type of radula. Secondly, and also in the Drilliinae, there is a muscular connection between the retractor muscle of the radular sac and the columellar muscle (Kantor, 1990). This is a condition found in some meso- and archaeogastropods, as for example in *Littorina*, *Cryptonatica* and *Tegula* (Fretter & Graham, 1963; Kantor, unpublished observations). In most other prosobranch gastropods, including those turrids where the buccal mass lies within the proboscis, this connection is broken and the radula is connected by muscles to the walls of the proboscis. Finally, the basal buccal mass is a character-state shared amongst most of the subfamilies of Turridae, along with the Terebridae, Pervicaciidae and Conidae.

b)   Buccal mass located within the proboscis
In *Clavatula diadema* (Clavatulinae), the buccal mass lies within the proboscis, but in a proximal position (Kantor, 1990, fig. 8). In *Clionella sinuata* (Clavatulinae), *Pilsbryspira nympha* (Zonulispirinae) and *Funa latisinuata* (Crassispirinae), it lies more anteriorly, about half way along the proboscis (Figs 6 & 14). In *Strictispira paxillus* (Strictispiri-

nae) (Fig. 13), *Toxiclionella tumida* (Clavatulinae) (Kantor, 1990 fig. 4), and *Turricula nelliae spurius* (Cochlespirinae) (Taylor, 1985; Miller, 1990), the buccal mass lies in a distal position near the tip of the proboscis.

The distally shifted position of the buccal mass in these few turrids is a derived condition, being found only in some species of the subfamilies Clavatulinae, Cochlespirinae Zonulispirinae and Strictispirinae.

c)   Buccal mass situated a long way to the posterior of the proboscis base (Kantor, 1990, fig. 1).
This condition is found only in *Hormospira* (Pseudomelatominae) and described by Kantor (1988).

## Elongation of the oesophagus to the anterior of the circum-oral nerve ring

In some turrids the oesophagus is elongated into a curved loop between the base of the proboscis and the circum-oral nerve ring (Fig. 14). This elongation is found in those turrids with a buccal mass situated within the proboscis, and allows forward movement of the buccal mass on protraction of the proboscis. This condition is found in Clavatulinae, Strictispirinae, *Turricula nelliae spurius* (Cochlespirinae), Crassispirinae such as *Funa latisinuata*, and *Pilsbryspira* (Zonulispirinae).

## Buccal lips (inner buccal tube)

These consist of muscular extensions of the anterior walls of the buccal mass, which protrude as a tube into the lumen of the buccal tube (Figs 1 & 9). In *Oenopota levidensis* where the buccal lips are long (Shimek, 1975), they form a second 'proboscis' within the true proboscis. At full contraction of the true proboscis, the tube formed by the buccal lips protrudes through the mouth. Shimek (1975) called this secondary 'proboscis' the buccal tube. Various developments
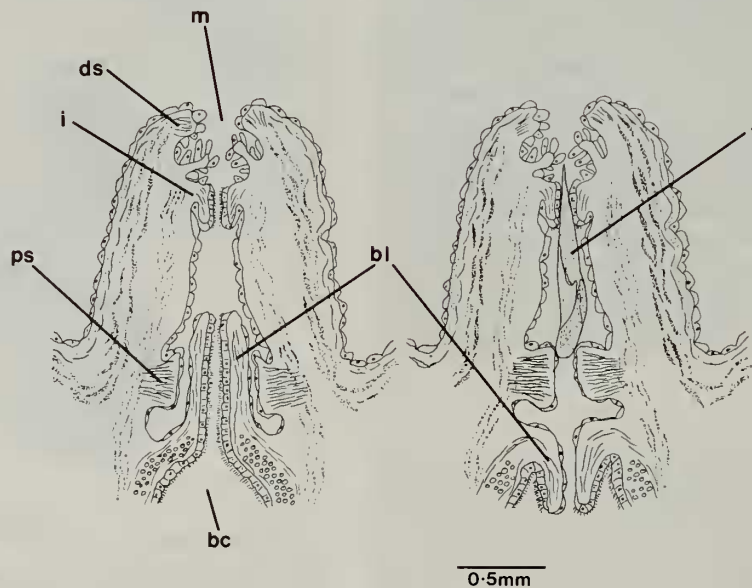


Fig. 9   *Mangelia nebula*; longitudinal section through the proboscis. A, with buccal lips protracted; B, radular tooth in proboscis and buccal lips withdrawn into the buccal cavity. After Sheridan *et al.* (1973, fig. 7) & Delaunois & Sheridan (1989, plate II). Abbreviations: bc, buccal cavity; bl, buccal lips; ds, distal sphincter of buccal tube; i, buccal tube introvert; m, mouth; ps, posterior sphincter of buccal tube; t, radular tooth.
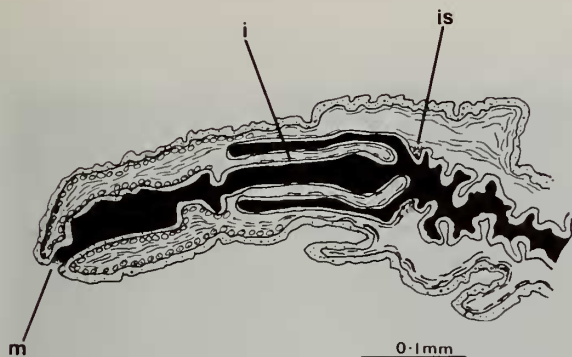
**Fig. 10**  *Eucithara stromboides*; longitudinal section through the anterior end of the proboscis showing the buccal tube introvert. Abbreviations: i, introvert; is, intermediate sphincter; m, mouth.



**Fig. 11**  *Turricula nelliae spurius*; extended proboscis, showing the inner ring of the protrusive lips. Scale bar = 100 μm.

of the buccal lips from a short tube to long proboscis-like structures, are seen in species of the subfamily Mangeliinae. Sections of *Mangelia nebula* (Sheridan *et al.*, 1973; Delaunois & Sheridan, 1989) show that the buccal lips can be inverted into the buccal cavity (Fig. 9b). In the genus *Aforia* (Cochlespirinae), some species have well developed buccal lips, but in others they are absent (Sysoev & Kantor, 1987).

In some conoideans lacking a proboscis and radula (e.g. *Terebra gouldi* (Miller, 1975)), the buccal lips are enlarged and consist only of circular muscles. They have the appearance of, and may be confused with, the true proboscis.

## The buccal cavity and radular apparatus

From the true mouth, the buccal tube leads to a well-defined chamber, the buccal cavity, which is surrounded by thick walls of circular muscle. The radular diverticulum usually opens ventrally into the buccal cavity. It consists of the radular sac within which the radular teeth are formed, and in less-derived turrids, an odontophore and sublingual pouch (Fig. 15). The latter is the site where degeneration of the radular teeth and ribbon occurs. The buccal sac is defined (Shimek, 1976), as that part of the radular diverticulum that lies between the buccal cavity and the entrance of the salivary ducts.

In higher turrids without a radular membrane and odontophore, the sublingual pouch is transformed into a caecum for the storage of radular teeth prior to their use at the proboscis tip.

### Radula caecum (often called short arm of the radula sac)

This is a diverticulum which branches off the anterior end of the radular sac, in which detached radular teeth are stored prior to their use at the proboscis tip (Fig. 15). We regard this structure as a homologue of the sublingual pouch found in other gastropods with a radular ribbon. A radular caecum is present in higher turrids, for example the subfamilies Mangeliidae, Daphnellinae, and Borsoniinae and also in Conidae and some Terebridae.

Shimek (1976) showed that the caecum in *Oenopota levidensis* is divided longitudinally by a septum. We have seen this structure only in *Micantapex parengonius* (Borsoniinae).

### Radular membrane

In general, the 'lower' turrids have a robust radular membrane, whilst in 'higher' turrids, it is thin or absent. However, even in 'lower' turrids, the strength of the membrane varies considerably between taxa and we recognise only the presence or absence of the membrane as a functionally important character.

A radular membrane is absent in the subfamilies Borsoniinae, Mangeliinae, Daphnellinae, Conorbinae, Clathurellinae, Taraniinae, Conidae and most Terebridae.

### Odontophore

An odontophore with cartilages is present in many lower turrids (Drilliinae, Pseudomelatominae, Strictispirinae, Clavatulinae, Turrinae, Cochlespirinae, Crassispirinae), the Pervicaciidae, and a few species of *Hastula* (Terebridae), but is absent in higher turrids, Conidae and most other Terebridae.

If an odontophore is present, then the cartilages may be either fused, or separated at the anterior end. If the cartilages are separated, they are joined by a muscular connection. We have seen fused odontophoral cartilages in *Lophiotoma*, Pseudomelatominae, *Splendrillia*, *Clavus sp.*, *Inquisitor* and *Funa* spp., *Toxiclionella* and some *Aforia* species. Two separate cartilages are usually present in species of Clavatulinae (except *Toxiclionella*), *Strictispira paxillus* (Strictispirinae) (Fig. 13). In *Aforia lepta* (Cochlespirinae), only the muscle is present, over which the radular membrane bends (Sysoev & Kantor, 1988).
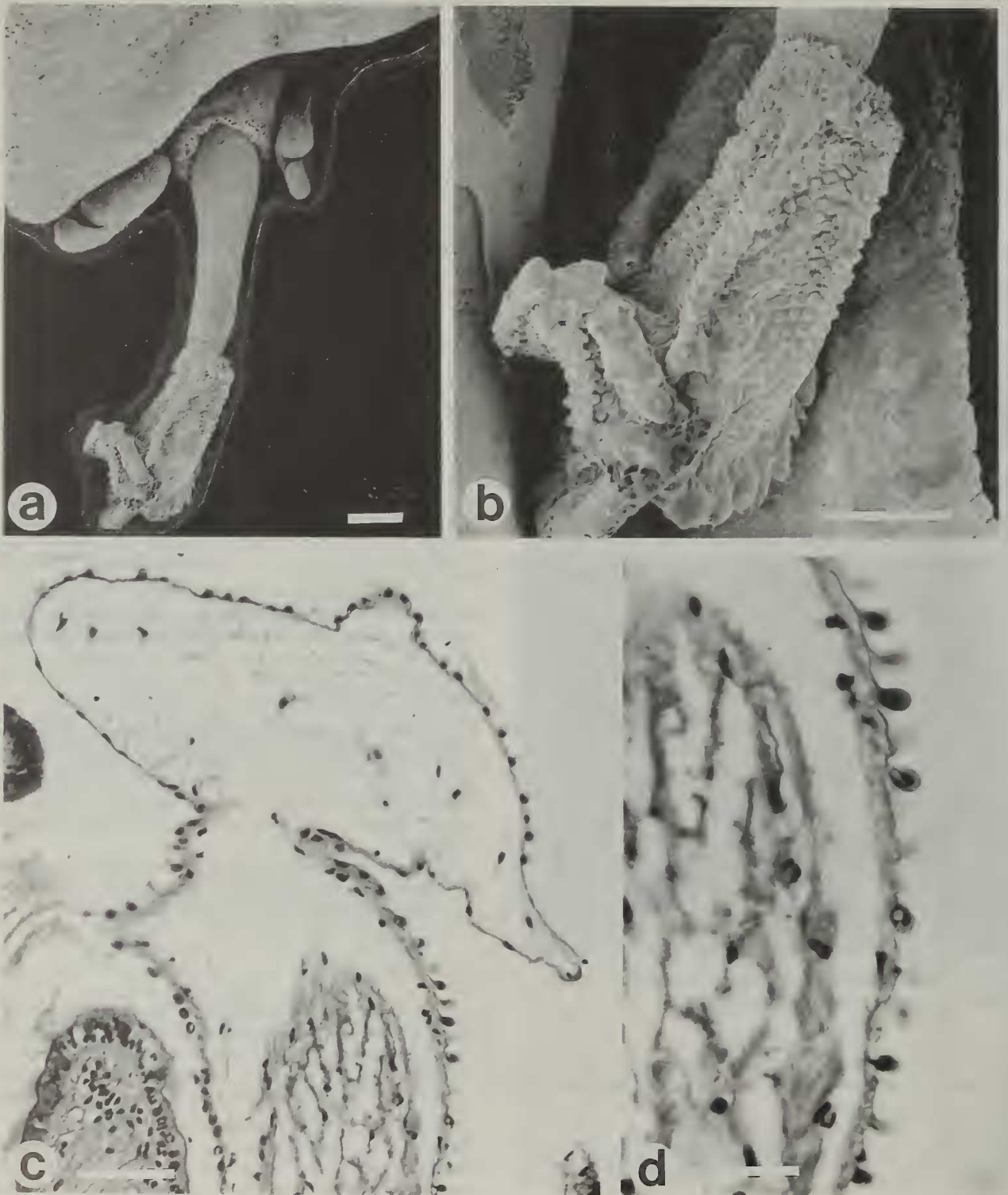
**Fig. 12** *Mangelia powisiana*; a, relaxed specimen showing sac-like structure at distal end of extended proboscis. Scale bar = 100 μm. b, detail of sac body with warty external surface. Scale bar = 100 μm. c, section of the sac showing the thin epithelium with granule structures produced by single cells with large nuclei. Scale bar = 50 μm. d, detail of c. Scale bar = 10 μm.

## Radula

The radula has been by far the most studied of the organs of the foregut and there are many published illustrations of conoidean radular teeth (e.g. Powell, 1966; McLean, 1971; James, 1980; Bandel, 1984; Bogdanov, 1990; Nybakken, 1990 and Taylor, 1990). Shimek & Kohn (1981) classified turrid radulae into a number of functional groups and attempted a cladistic analysis of radular characters. However, amongst the 'lower' turrids there is little evidence from direct observations to support their functional categories. Indeed, recent evidence shows that even in the least-derived radulae which possess a strong radular ribbon, the marginal teeth can be held singly at the proboscis tip in a stabbing position (Kantor & Taylor, 1991).

A radula is present in most Turridae, all Conidae, possibly all Pervicaciidae and some Terebridae. It is absent in some species of Daphnellinae, Taraninae and many species of Terebridae (Miller, 1970; Taylor, 1990). The phenomenon of radula-loss in conoideans has recently been reviewed by Kantor & Sysoev (1989).

For the purposes of the present analysis, we have attempted to recognise different morphological types of radula, without any functional interpretation.

The radula of the Drilliinae, which is usually regarded as the least-derived condition within the Turridae, has five teeth in each transverse row (Fig. 16a). These teeth are usually refered to as central, lateral and marginal teeth respectively; although there are different interpretations (Kantor, 1990; Starobogatov, 1990). We consider the morphology of each of these teeth in turn.

### 1.  Central tooth

A central tooth is present in species of Drilliinae, Pseudome-latominae, Turrinae, Clavatulinae, and Cochlespirinae. It can be reduced and lost in some species of these subfamilies except Pseudomelatominae. (i) In the Pseudomelatominae, the central tooth is fairly robust and broad, with a large curved central cusp and sometimes smaller cusps at either edge (Fig. 17e & f). (ii) In the Drilliinae the central tooth is robust, but small and narrow (Fig. 16b & d), usually with a prominent central cusp and a number of subsidiary cusps. (iii) In the Turrinae and Clavatulinae (Figs 18a–d, 19a & b), the central tooth appears broad, but apart from a spine-like central cusp is poorly defined. The central cusp appears homologous with the central tooth of the Drilliinae, but the insubstantial, lateral 'wings' may represent vestiges of lateral teeth which have fused with the central tooth. Alternatively, the whole tooth might be homologous with the central tooth of the Pseudomelatominae, the central cusp remaining prominent, but the lateral edges becoming less substantial. Study of the ontogeny of the radula in these taxa might distinguish between these alternative possibilities.

### 2.  Lateral teeth

We recognise two types of lateral teeth. (i) In what is considered to be the least-derived condition, most species of Drilliinae have large, multicuspidate, comb-like, lateral teeth (Fig. 16a,c,e). However, reduced teeth are found in some drilliine species (Bandel, 1984, fig. 306). (ii) In *Antiplanes* (Cochlespirinae), the radula folds along the middle of the radular ribbon, suggesting that the poorly defined, plate-like teeth are in fact laterals (Kantor, 1990; Kantor & Sysoev, 1991, figs 26–27, 30–32). These 'teeth' were not visible on S.E.M. preparations. Similar, poorly defined, lateral 'teeth' are also present in optical preparations of *Crassispira* and *Crassiclava* of the Crassispirinae (Maes, 1983 fig. 31 & 37, p. 322; Kilburn, 1988, p. 239).

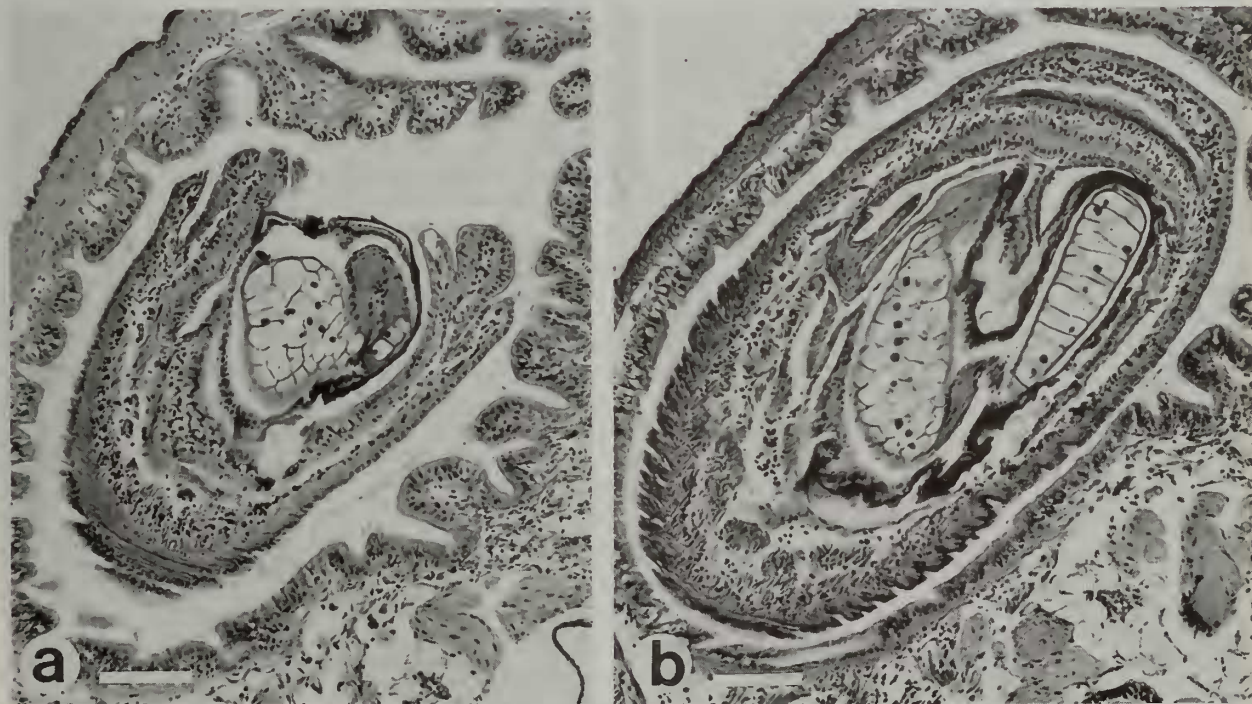In all other subfamilies of Turridae, Pervicaciidae, Terebridae and Conidae, lateral teeth are absent.



**Fig. 13**  *Strictispira paxillus*; transverse section of the rhynchoel and the proboscis tip. a, mouth with distally-situated radula and virtually no bucal tube. Scale bar = 100 µm. b, section of the proboscis slightly to the posterior of (a) showing the two large odontophoral cartilages. Scale bar = 100 µm.
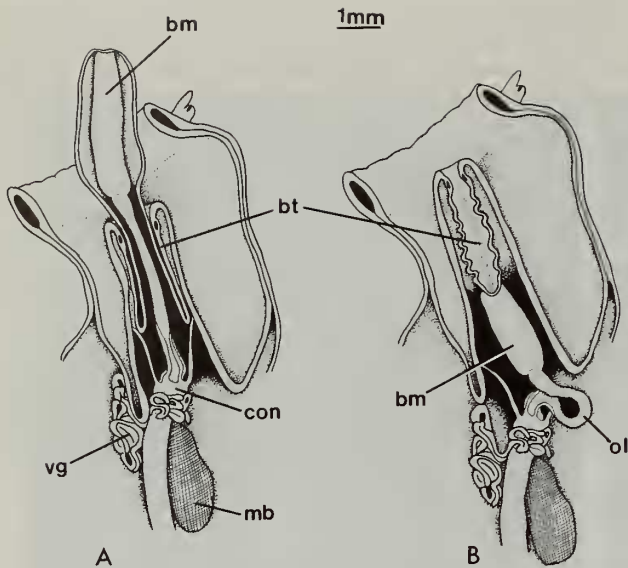
Fig. 14 *Funa latisinuata*; anterior alimentary system. A, proboscis with buccal mass in extended position; B, with buccal mass in retracted position and showing the loop of the oesophagus situated to the anterior of the nerve ring. Modified from an unpublished drawing by J. Miller. Abbreviations: bm, buccal mass; bt, buccal tube; con, circum-oral nerve ring; mb, muscular bulb; ol, oesophageal loop; vg, venom gland.
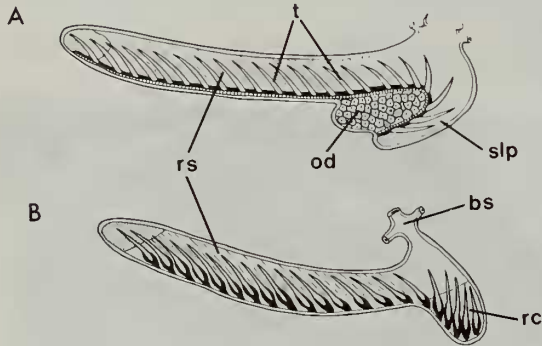


Fig. 15 Diagrammatic section through the radular sac. A, in turrids possessing an odontophore; B, turrids lacking an odontophore, but with a radula caecum. Abbreviations: bs, buccal sac; od, odontophore; rs, radular sac; rc, radula caecum; slp, sublingual pouch; t, radular teeth. Buccal sac is that portion of the radular sac lying between the entrance of the salivary ducts and the buccal cavity.

3.  Marginal teeth

In most conoideans the marginal teeth are the principal functional teeth. Although diverse in appearance, they can be divided into three broad categories of solid, wishbone and hollow. There may be several subdivisions of each category. Teeth of the first category are represented by a single, flat, distally acute plate. Wishbone teeth are characterised by two plates connected to each other. Hollow teeth are distinguished by a cavity within the tooth.

a)  Solid marginal teeth

We recognise four main categories of solid teeth. (i) Simple, flat teeth, often with a simple, blunt barb (Figs 16a, f, Fig. 20a). This type of tooth is common in the Drilliinae. (ii) Simple teeth as in (i), but with the lateral edges of the tooth curved to form a channel or gutter. This type of tooth has been recorded from *Drillia cydia* (Powell, 1966, fig 81; Maes, 1983, fig. 28). (iii) Simple, solid teeth, which are curved and pointed (Fig. 17e). This type of tooth is found only in Pseudomelatominae (Kantor, 1988) and the Pervicaciidae (Taylor, 1990).(iv) Simple, awl-shaped teeth with a large base and pointed tip and a spathulate process midway along the tooth (Figs 17a–d). This type of tooth has been found only in the subfamily Strictispirinae.

b)  Wishbone teeth (sometimes called duplex teeth)

In this type of dentition, the marginal teeth consist of two parts, comprising the main tooth together with an accessory limb. Published illustrations suggest a great variety of form in wishbone teeth, but S.E.M. observations show that some of this variety results from artifacts produced by the transparency of light microscopy and by different positions of teeth (often with displaced tooth parts) in preparations.

We recognise four basic types of wishbone teeth:

(i) Broad, slightly curved teeth, sometimes with a blunt barb (Fig. 20 b–d). The lateral edges of the teeth are thickened, with a thin accessory limb attached to the main tooth at the anterior and posterior ends. This type of tooth is common in some Crassispirinae such as *Inquisitor*, *Paradrillia* and *Funa*, where the size and shape of the accessory limb varies considerably between species (Kilburn, 1988). Because the main limb is similar to the marginal teeth of the Drilliinae, we suggest this as the least-derived type of wishbone tooth. (ii) The teeth of this type are robust, short and curved, sometimes with a knife-like cutting edge on the main limb and a large accessory limb (Figs 18a,c; 19a,d). Teeth of this type are found in species of Turrinae, Clavatulinae, and Cochlespirinae. (iii) Teeth that may be modified wishbone teeth have been illustrated for *Ptychobela nodulosa* and *P.suturalis* by Kilburn (1989, figs 17–19). The teeth are awl-shaped without barbs, with apparently two nearly equisize limbs joined to form a central channel. An S.E.M. study of these teeth is needed to claify their morphology. (iv) In the radula of *Ptychobela griffithi* the teeth appear to be robust and solid with a simple barb (Fig. 22a), but they may in fact

Fig. 16 Radulae of Drilliinae. a, half radula row of *Clavus* sp. from Guam showing blade-like marginal teeth, comb-like lateral teeth and the small central tooth. Scale bar = 50 μm. b, central tooth of *Clavus unizonalis*. Scale bar = 5 μm. c, central and part of lateral teeth of *Spirotropis monterosatoi*. Scale bar = 20 μm. d, central tooth of *S. monterosatoi*. Scale bar = 10um. e, single lateral tooth of *S. monterosatoi*. Scale bar = 20 μm. f, marginal teeth of *S. monterosatoi*. Scale bar = 20 μm.

Fig. 17 Radulae of Strictispirinae and Pseudomelatominae. a, radula of *Strictispira paxillus*. Scale bar = 50 μm. b, marginal teeth of *Strictispira stillmani*. Scale bar = 50 μm. c, radula of *Cleospira ochsneri*. Scale bar = 50 μm. d, marginal teeth of *Strictispira paxillus* seen from side. Scale bar = 50 μm. e, radula of *Pseudomelatoma penicillata*. Scale bar = 100 μm. f, central tooth of *P. penicillata* seen from side. Scale bar = 10 μm. (*see* p. 138)

**Fig. 18**  Radulae of Clavatulinae and Cochlesprinae. a, *Clionella sinuata*; wishbone marginal and small central teeth. Scale bar = 50 μm. b. *Clionella sinuata* small central tooth. Scale bar = 10 μm. c. *Turricula nelliae spurius*, radula with wishbone marginal teeth and central tooth with spine-like cusp and lateral flanges. Scale bar = 50 μm. d. *T. nelliae spurius* central tooth. Scale bar = 5 μm.
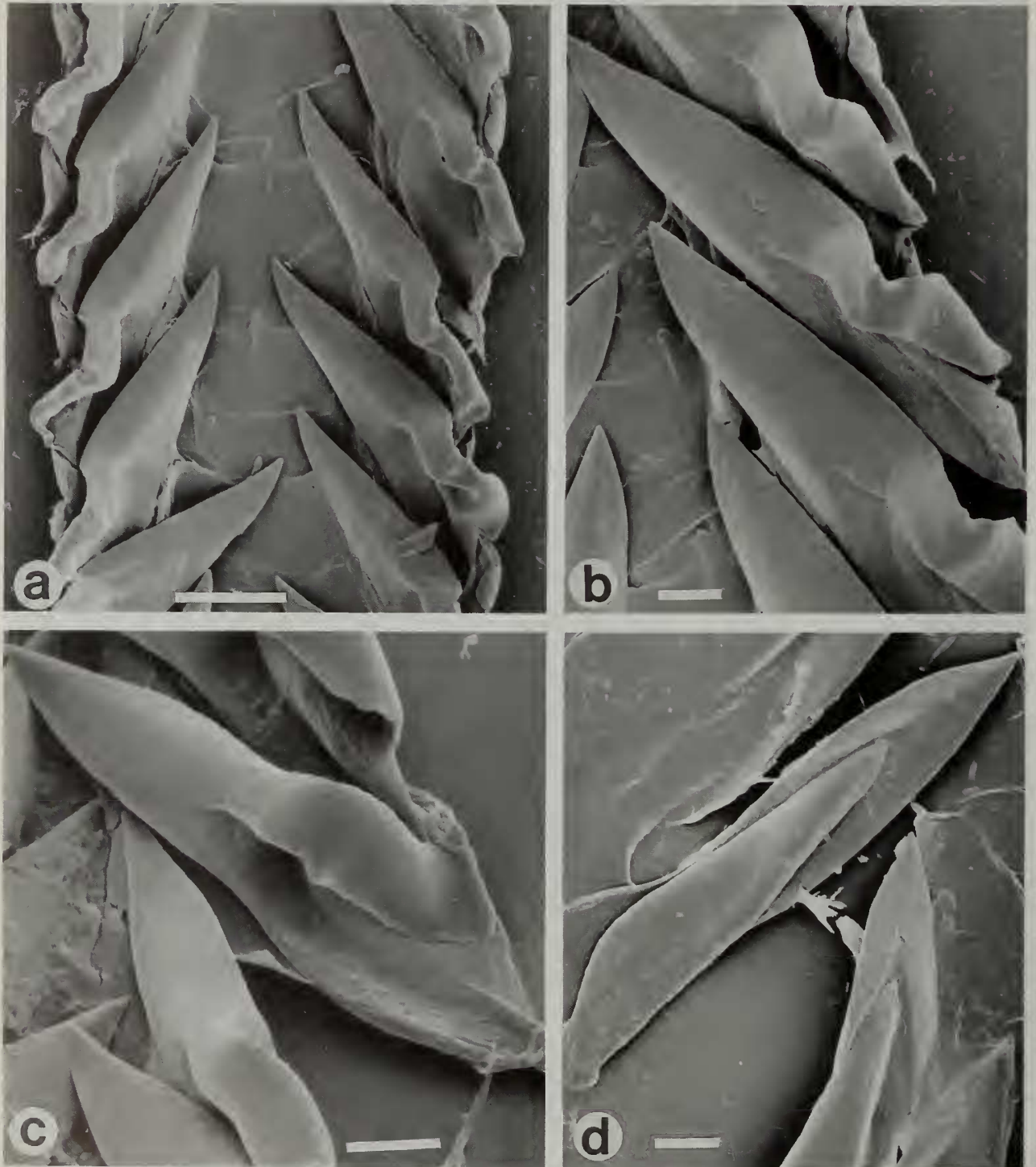
Fig. 19  Wishbone teeth of Turrinae and Cochlespirinae. a. radula of *Gemmula deshayesi*. Scale bar = 50 μm. b. marginal tooth of *Gemmula deshayesi* Scale bar = 20 μm. c. marginal tooth of *Lophiotoma acuta* Scale bar = 10 μm. d. marginal tooth of *Antiplanes sanctiioannis*. Scale bar = 20 μm..

be formed from two pieces as in *Ptychobela suturalis* (see above). Lack of material precluded further study of this and the type iii wishbone teeth.

c) Hollow teeth

There is a great diversity of detailed variation in the form of hollow marginal teeth even within a single genus (see for example, James (1980) and Nybakken (1990) for *Conus* and Bogdanov (1990) for *Oenopota*). However, for the purposes of this analysis we recognise only five main types of hollow teeth. (i) Teeth of this type are long, slender, and enrolled,

with a small base. The base is not differentiated morphologically and is not solid. The distal end of the tooth may be simple, or more or less, elaborately barbed (Figs 22e,g). There is an opening near the distal tip and a second opening placed more or less terminally at the proximal end. The shaft of *Hastula hectica* is perforated by holes (Taylor, 1990, fig. 2). For some *Conus* species, Nybakken (1990) has shown that during ontogeny, the hollow, rolled teeth develop from open, guttered forms and become progressively more elaborately barbed. Hollow teeth of Type i are found in species of
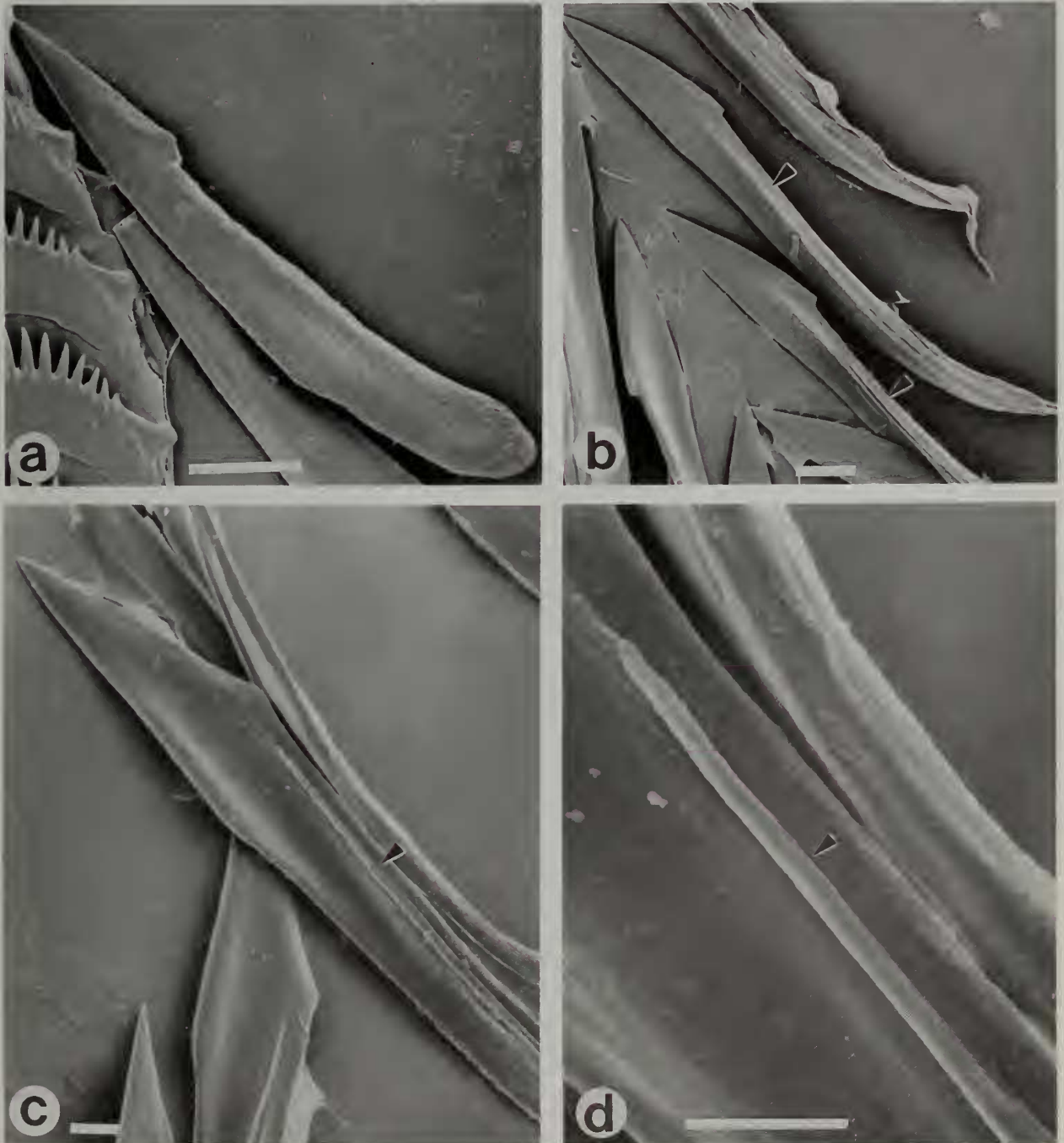


**Fig. 20.**   Radulae of Clavinae and Crassispirinae. a. marginal tooth of *Drillia rosacea*. Scale bar = 50 μm. b. *Funa latisinuata*; blade-like marginal teeth with thin accessory limb. Scale bar = 50 μm. c. *Vexitomina garrardi*; part of blade-like marginal tooth with accessory limb (arrowed). Scale bar = 10 μm. d. enlargement of (d) showing accessory limb. Scale bar = 10 μm.

Borsoniinae, Clathurellinae, *Toxiclionella* (Clavatulinae), Conidae, and Terebridae (ii) Hollow teeth of this second type are often short with a large, solid base (Fig. 23). The tooth cavity opens laterally between the shaft and the base. There are frequently side projections around the base (hilted dagger form of Powell 1966), often with a large irregular solid 'root' projecting from the base (Fig. 23e,f). These teeth are often only partially enrolled. Barbs may be present. Marincovich (1973) records rows of holes in the teeth of *Agathotoma ordinaria* (Mangeliinae). Teeth of Type ii are found in the subfamilies Mangeliinae, Oenopotinae (Bogdanov, 1990, figs 407–438), Thatcheriinae, and the radulate Daphnellinae. (iii) Teeth of this type are partially enrolled at the base, but solid and blade-like in the distal part (Fig. 22b). This type of tooth is presently known only from *Hastula bacillus* (Taylor & Miller, 1990). It may represent a transitional form between the solid teeth found in the Pervicaciidae and the hollow teeth of the Terebridae. (iv) This type of tooth is loosely enrolled to form a central channel, with a simple barb at the tip. The tooth was first described in detail from *Imaclava unimaculata* (Clavinae) by Shimek & Kohn (1981 fig. 7). *Imaclava* otherwise has comb-like lateral teeth as in typical Clavinae. Similar teeth are present in other species of *Imaclava* (McLean, 1971, fig. 7). (v) Enrolled teeth with a complex appearance are seen in *Pilsbryspira nympha* (Zonulispirinae) (Fig. 21). Although these are hollow teeth with a small barb, the shaft is complex and appears to be formed by partial enrolling of two units (Fig. 21b). The tooth may be derived by the enrolling of the elongate wishbone teeth typical of the Crassispirinae. (vi) Vestigial teeth, semi-enrolled, with a gutter along the tooth. Teeth of this type are considered by Bogdanov (1990) as

derived from the distal part of the shaft of Type ii teeth. This type of tooth is found in *Propebela turricula* and *P. harpularia* (Oenopotinae) (Bogdanov, 1990, figs 41, 433).

## Glands of the foregut

### Salivary glands

Salivary glands are present in most turrids, *Conus* and the radulate species of Terebridae and Pervicaciidae. In most species a pair of glands is present, but these may be fused together. The salivary ducts always open into either side of the buccal sac (Fig. 1). In *Turricula nelliae spurius*, which has a distal buccal mass, the salivary glands are contained within the proboscis and attached to the oesophagus (Miller, 1990).

In most conoideans, the salivary glands are acinous, but in the Mangeliinae, Thatcheriinae, Daphnellinae and *Haedropleura septangularis* (Crassispirinae) the glands consist of long, convoluted, single tubes (Sheridan *et al.*, 1973; own observations).

Turrids without a radula also lack salivary glands, but in the Terebridae, glands are present in some radula-less forms, such as *Terebra gouldi* and *T. maculata* (Miller, 1970, 1975).

### Accessory salivary glands

These are known in a few species of Turridae, some Conidae (Marsh, 1971; Schultz, 1983) and Terebridae (Taylor & Miller, 1990; Taylor, 1990). They have a similar histology to the accessory salivary glands found in other neogastropod families such as the Muricidae (Andrews, 1991). Further-
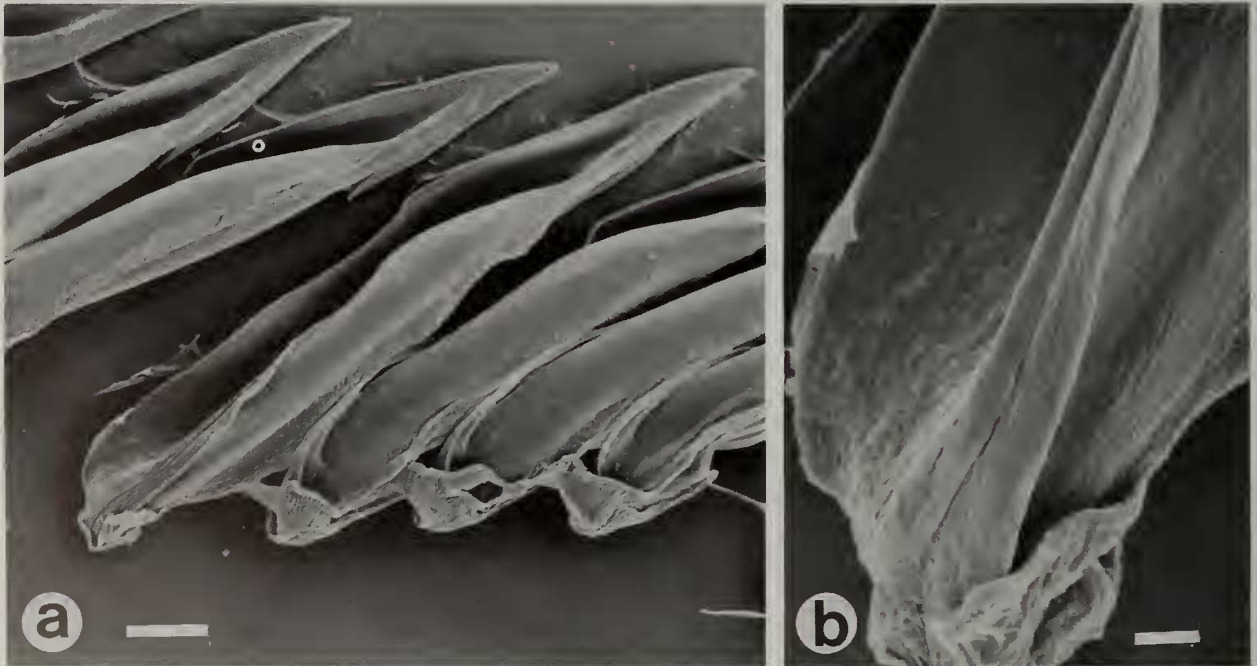


**Fig. 21.** Enrolled teeth of *Pilsbryspira nympha*. a. several adjacent marginal teeth. Scale bar = 25 μm. b. detail of base of tooth showing double structure (arrow) suggesting that tooth may be formed by the enrolling of wishbone teeth. Scale bar = 5 μm.

**Fig. 22** Single marginal teeth from Turridae and Terebridae. a. *Ptychobela griffithi*. Scale bar = 10 μm. b. *Hastula bacillus*. Scale bar = 5 μm. c. *Glyphostoma candida* Scale bar = 50 μm. d. enlargement of the tip of the *G. candida* tooth. Scale bar = 10 μm. e. *Genota mitraeformis*. Scale bar = 20 μm. f. *Terebra babylonia*. Scale bar = 20 μm. g. *Conus ventricosus* Scale bar = 20 μm.

more, the ducts from the accessory glands open near the tip of the buccal tube, which is the homologous position to that found in other neogastropods.

Within the Turridae, we have observed accessory salivary glands in only two subfamilies: the Borsoniinae (*Scrinium neozelanicum*, *Borsonia ochracea*, and *Micantapex parengonius*) and Cochlespirinae (*Aforia hypomela*, *A. kupriyanovi*, *A. abyssalis*). In the Terebridae, we have seen accessory glands in *Hastula bacillus*, *Terebra babylonia*, *T. funiculata* and *T. subulata* (Taylor, 1990). Usually, only a single gland is found, but two glands are present in *Terebra subulata*.

### Venom apparatus (venom gland and muscular bulb)

The long, tubular, and convoluted venom gland is the most conspicuous organ of the conoidean foregut. It always passes through the nerve ring and always opens into the buccal cavity immediately posterior to the opening of the radular sac (Figs 1 & 7). The venom gland is present in most conoideans, except the radulate *Strictispira* (Maes, 1983); *Gymnobela tincta*, which has a vestigial radula; the radula-less turrids from the subfamilies Daphnellinae and Taraninae (Smith 1967; Sheridan *et al.*, 1973; Kantor & Sysoev, 1989), the radula-less Terebridae (Miller 1975; Taylor, 1990) and the radulate Pervicaciidae (Taylor, 1990).

In some species, the histology of the venom gland changes in the anterior portion of its length, after its passage through the nerve ring. The posterior portion is packed with venom granules (Fig. 24), but the anterior portion is duct-like and ciliated (e.g. *Clavatula*, *Clionella*, *Turricula*, *Lophiotoma* and *Pilsbryspira*). This change in histology is usually correlated with the elongation of that part of the oesophagus lying between the nerve ring and buccal mass. In other conoideans, venom granules are present all the way along the length of the gland, sometimes even into the buccal cavity.

Extensive studies have been made of the composition and pharmacology of the venom in a few *Conus* species (review by Oliviera *et al.*, 1990). The composition of the venom is very complex and the results from these studies have a potential utility in phylogenetic analysis. However, no comparable studies yet exist for the Turridae and Terebridae.

### Muscular bulb

The muscular bulb (Figs 1 & 6) lies at the posterior end of the venom gland and is present in all those species possessing the gland. Differences between taxa are observed both in the number, orientation and relative thickness of the various muscular layers forming the wall of the bulb. The usual condition is of an outer, circular-muscle layer, a thin, middle connective tissue layer, with an inner longitudinal layer. We have, however, observed other configurations of the muscle layers. For example in *Mangelia* species and *Eucithara*, the outer muscular layer is very thin, but the inner layer very thick. *Daphnella reeveana* has only a single, thin muscle layer, whilst *Conus textile* has four distinct alternating circular and longitudinal muscle layers, three of them lying inside the connective tissue layer.

Additionally, Ponder (1970) mentions that he has observed glandular cells in the epithelium lining the muscular bulb in

*Lucerapex* (Turrinae) and *Maoritomella albula* (Borsoniinae). We have not observed the glandular cells in any turrid we have examined.

### Summary of foregut anatomy

From the foregoing discussion, it is clear that there is a great variety of foregut anatomy present within the Conoidea and considerable variation may be present even within species of one subfamily. As a summary, twelve of the main types of foregut configuration are shown diagramatically in Figs 25 & 26. It should be emphasized that only a relatively small number of conoidean species have been investigated anatomically and it is likely that further types of foregut remain undiscovered. Nevertheless, there are several anatomical characters which define the Conoidea and are present in most representatives (and in all the least derived groups). These are:-

1. The presence of a venom gland.
2. The buccal mass located at the base of the proboscis.
3. The proboscis formed by the elongation of the buccal tube.
4. The presence of a permanent rhynchodeum.
5. The tendency for the loss of central and lateral teeth from the primary five toothed radular row.

## FUNCTIONAL MORPHOLOGY OF THE DIGESTIVE SYSTEM AND FEEDING MECHANISMS IN TOXOGLOSSA

As has been outlined in the previous section, the morphology of the digestive system of Conoidea and especially that of the Turridae, is highly varied. These variations in morphology probably reflect differences in feeding behaviour and diet. Apart from *Conus*, conoidean diets are still very poorly known. Indeed, for in excess of 4000 living species of Turridae, feeding information is available for less than 30 species (reviewed by Miller, 1989). These data, derived mainly from gut content analysis, show that turrids feed mainly on errant and sedentary polychaetes and more rarely on other phyla such as sipunculans, nemerteans, and molluscs. Very few direct observations of the feeding process in the Turridae have been made (Pearce, 1966; Shimek, 1883a, b, c; Shimek & Kohn 1980; Miller, 1990). Because of this lack of information, our conclusions concerning the feeding mechanisms of Turridae are based upon analysis of the morphology of the digestive tract and by comparison with species whose feeding mechanism is known.

Our classifications of feeding mechanisms is based upon the following characters listed in order of priority: the presence/absence of venom apparatus (used for immobilizing or killing the prey); the mode of radula function ( which may be used solely as a whole organ, as a whole organ with simultaneous use of separate teeth, or as separate teeth only at the proboscis tip); position of the buccal mass (either basal or shifted anteriorly towards the proboscis tip). We recognize

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**Fig. 23** Hypodermic-type marginal teeth with a large solid bases. a. *Paramontana* sp. Scale bar = 2 μm. b. *Propebela rugulata*. Scale bar = 10 μm. c. & d. *Thatcheria mirabilis* Scale bars = 20 um. e.& f. *Mangelia powisiana*. Scale bars = 5 μm G. *Eucithara stromboides*. Scale bar = 10 μm.
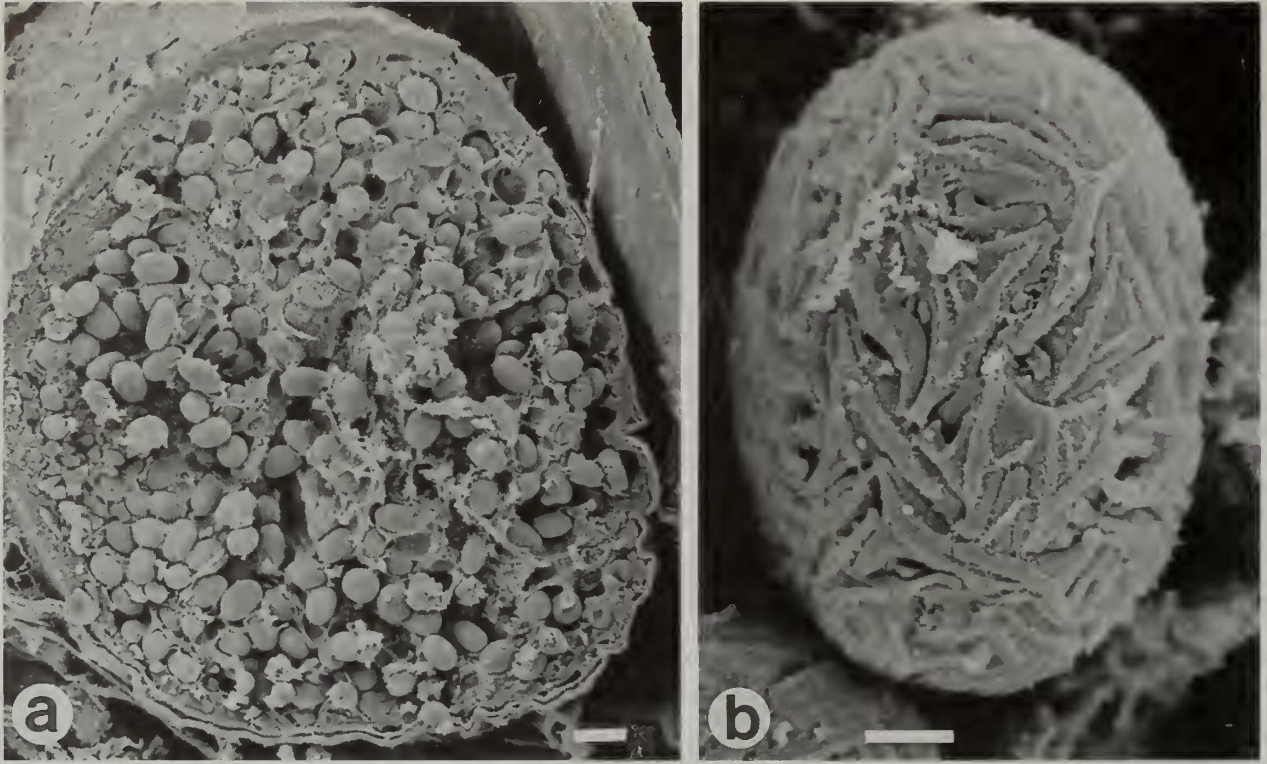
**Fig. 24**  Venom gland of *Clavus* sp. Guam. a. section through critical-point dried venom gland showing venom granules. Scale bar = 10 μm
b. enlargement of single venom granule. Scale bar = 1 μm.

five main and several sub-types of feeding mechanism. Some of these have already been described (Kantor & Sysoev, 1990; Kantor, 1990), but are here partially revised and corrected.

# I. Venom gland present

## Feeding mechanism Type 1

The first functional type of digestive system and feeding mechanism, that in which the radula is used only as a whole organ in conjunction with the venom apparatus is found among species of Pseudomelatominae and in *Toxiclionella tumida* (Clavatulinae) and can be subdivided into two sub-types.

The first sub-type is characteristic of the Pseudomelatominae, an endemic subfamily from western central America, which includes 3 genera and several species (McLean in Keen, 1971). The anatomy of two species *Pseudomelatoma penicillata* and *Hormospira maculosa* indicates the isolated position of the group among Conoidea (Kantor, 1988). This is particularly clear, from the radular morphology, which consists of a large and well developed central tooth, flanked by large, scythe-like, but solid, marginal teeth.

The buccal mass is situated either at the proboscis base and far ahead the nerve ring in *Pseudomelatoma penicillata*, or in front of the nerve ring and distant from the proboscis base in *Hormospira maculosa*. The anterior part of the digestive tract forms a long curve, either by the elongation of that part of the oesophagus between the nerve ring and the buccal mass (*P. penicillata*), or by the elongation of the posterior part of the buccal tube (*H. maculosa*).

Both species have a well-developed venom gland and although the diet of Pseudomelatominae is unknown, the presence of the large venom gland indicates the predatory mode of feeding. The gastropods also have a muscular proboscis with a wide oral opening but without a sphincter. The absence of the oral sphincter, which is usually used for holding single radular teeth at the proboscis tip (Kantor & Taylor, 1990), coupled with the curved form of the marginal teeth, indicate that the gastropods do not use separate teeth for stabbing the prey. Kantor (1988) supposed that prey capture occurs with the aid of the proboscis tip and is facilitated by the wide and highly extensible oral opening. If this is so, then envenomation of the prey should occur within the anterior part of the proboscis. This facilitates the transport of prey into the buccal cavity, by the peristaltic movements of well-developed circular muscles of the buccal tube.

However, the presence of the elongated part of the oesophagus between the buccal mass and nerve ring in *P. penicillata* may indicate another mode of prey capture. In some turrids (e.g. *Funa latisinuata*, Fig. 14), the presence of such an elongation of the oesophagus is connected with the ability to evert the buccal mass, with the radula, through the proboscis and mouth. It is possible, that *P. penicillata* can evert the buccal mass through the mouth and use the radula directly in prey capture. Envenomation would in this case occur through the damage to the prey made by the radular teeth. Also the very large odontophore (the largest of all the turrids studied) suggests that the radula may also tear the prey.

The morphology of *Hormospira* differs from that of *Pseudomelatoma*, in that the curve is formed by the posterior part of the buccal tube and elongated buccal mass. The
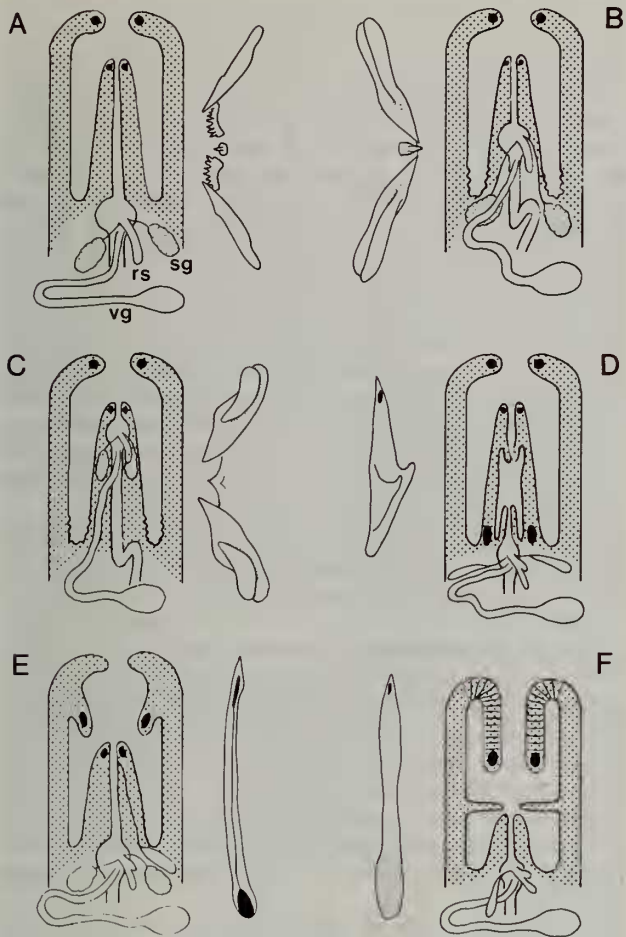
**Fig. 25** Diagram (with Fig. 26) summarizing some of the major types of foregut morphology found amongst the Conoidea, with radulae, where present, illustrated alongside. Not to scale. A. *Clavus unizonalis*; B. *Clionella sinuata*; C. *Turricula nelliae spurius*; D. *Mangelia nebula*; E. *Ophiodermella inermis*; F. *Daphnella reeveana*. Abbreviations: asg, accessory salivary glands; sg, salivary glands; rs, radular sac; vg, venom gland; black dots are sphincters.

**Fig. 26** Further types of foregut morphology found in the Conoidea. G. *Gymnobela emertoni*; H. *Philbertia linearis*; I. *Conus ventricosus*; J. *Duplicaria spectabilis*; K. *Terebra subulata*; L. *Terebra maculata*.

radular sac is located far behind the base of the proboscis. Therefore, it is doubtful that the buccal mass can be everted through the mouth opening. This species probably catches prey using the proboscis tip. Envenomation could occur either by the squirting of venom through the mouth, when the proboscis is in contact with the prey, or in the anterior part of the proboscis, when the prey is partly swallowed. In either case the radula is not used to envenomate the prey and is either used for further transportation in the oesophagus of for partial tearing of prey tissue.

The second sub-type is found in *Toxiclionella tumida* and differs from the first in that the buccal mass is located near the proboscis tip (Kantor, 1990, fig. 4), which has no distal sphincter. This species is characterized by a radula formed of hollow, and barbed marginal teeth (Kilburn, 1985, fig. 14), which are attached all along their length to the radular membrane. The hollow radular teeth are similar in morphology to those of higher conoideans. The gastropod has a long venom gland and in the posterior part of the proboscis there is a single salivary gland with paired ducts. The radular teeth are sufficiently long, that during protraction of the odonto-

phore, the tips would protrude through the oral opening, and thereby stab the prey.

A comparable mechanism may occur in *Turricula nelliae spurius* (Taylor, 1985), which has the buccal mass located in a similar distal position in the proboscis to that of *T. tumida*, and during feeding can protrude the odontophore through the mouth opening (Miller, 1990). But *T. nelliae* possesses a sphincter in the anterior part of the buccal tube, and this feature usually correlates with the use of separate marginal teeth for stabbing (Kantor & Taylor, 1991).

In conclusion, we suggest that a similar type of feeding mechanism evolved independently in *Pseudomelatoma* and *Toxiclionella*. In the former, the primitive character of the radula suggests that the feeding mechanism is primary; whilst in *Toxiclionella* it is probably a secondary feeding mode when compared with other members of the subfamily. It is possible that with the shift of the buccal mass to the proboscis tip, *Toxiclionella* lost the mechanism of stabbing the prey with single marginal teeth and instead protrudes the radula through the mouth and uses the hollow teeth which remain firmly anchored to the radular membrane.

*Feeding mechanism Type 2*

The second feeding mechanism is typical of the majority of 'lower' turrids and the terebrid *Hastula bacillus*, which possess a well developed radular membrane and lack a radular caecum. The characteristic feature of this mechanism is the use of separate marginal teeth at the proboscis tip for stabbing the prey, whilst the radula is also used as a whole organ for different purposes (Sysoev & Kantor, 1986, 1989).

The use of single marginal teeth at the proboscis tip by turrids having radulas with well developed subradular membranes has been demonstrated in representatives of all 7 subfamilies of 'lower' Turridae (excepting the Pseudomelatominae) and also the terebrid *Hastula bacillus* (Kantor & Taylor, 1991).

According to the position of the buccal mass this type may be divided into two sub-types. Gastropods of the first subtype have the buccal mass situated at the proboscis base. These include species of Drilliinae, Cochlespirinae, Turrinae and many Crassispirinae. In these gastropods, the solid or wishbone marginal teeth, which become detached from the membrane during its degeneration in the sublingual pouch, are used at the proboscis tip for stabbing the prey. It should be noted, that separate teeth were not found in the sublingual pouch, therefore it does not serve for the storage of teeth. Meanwhile, the radula as a whole organ probably has a different function within the buccal cavity. This is most likely for the transport of food from the cavity to the oesophagus. Some evidence for this comes from the observations of Maes (1981), who noted the presence of intact sipunculans in the posterior part of the oesophagus of *Drillia cydia* (Drillinae). Although at first sight, it might be thought that the large, pectinate, lateral teeth found in this species might serve for tearing or rasping the prey.

A characteristic feature of the proboscis is the presence of the sac-like enlargement of the anterior part of the buccal tube and a well-developed, distal sphincter(s). Gastropods of this group lack a radular caecum, so they can use only teeth which are sporadically detached from the membrane. Either the marginal teeth are not used in every feeding act, or, the teeth are held at the proboscis tip for a long time. That is, from the moment of their detachment from the subradular membrane to the next feeding act. We have found teeth at the proboscis tip in sections of 'lower' turrids much more frequently, than in the 'higher' turrids. Moreover, in *Splendrillia chathamensis*, in addition to the normal buccal sphincters of the buccal tube, teeth are attached by their base to a 'mat' of epithelial cells in the enlargement of the buccal tube (Kantor, 1990, fig. 3). Such a mechanism of tooth fixation confirms the long-term presence of the tooth at the proboscis tip. Thus, the enlargement of the anterior part of the buccal tube, could be considered as a functional analogue of the radular caecum.

The use of marginal teeth at the proboscis tip, in turrids with a well-developed radular membrane, explains how hollow, marginal teeth might have evolved independently in different groups possessing the radular membrane and odontophore. For example, *Imaclava* (Drillinae) (Shimek & Kohn, 1981), has hollow teeth and most probably uses these at the proboscis tip for stabbing the prey in a manner similar to that of higher Conoidea.

The second feeding sub-type is seen in *Funa latisinuata* (Crassispirinae), which feeds upon nemerteans. From dissection of relaxed animals, Miller (1989, fig 6f) showed that in the everted position, the buccal mass with the radula is protruded through the mouth opening (Fig. 14a). In sections of animals with a contracted proboscis, the buccal mass lies towards the base. It is known that this species uses the marginal teeth at the proboscis tip (Kantor & Taylor, 1991). Thus, the mode of feeding may be reconstructed as follows. After stabbing the prey, the gastropod everts the buccal mass, with the walls of the buccal tube, through the mouth opening and picks up the prey with the protruded radula. With retraction of the buccal mass, the prey is pulled into the proboscis. Correlated with this feeding mechanism, is the elongation of the anterior oesophagus between the buccal mass and the circum-oral nerve ring. During protraction of the buccal mass, the oesophagus should be pulled through the nerve ring. But, as the nerve ring in Conoidea is highly concentrated, and usually tightly attached to the oesophagus, the only possibility is the elongation of the oesophagus itself anterior to the nerve ring, forming a loop, which is straightened during eversion of the buccal mass (Fig. 14b).

In addition to *Funa latisinuata*, this elongation of the oesophagus between the buccal mass and the nerve ring has been found in species from several different subfamilies of Turridae–Pseudomelatominae, all Clavatulinae, *Pilsbryspira nympha* (Zonulispirinae), *Vexitomina* (Crassispirinae), *Turricula nelliae spurius* (Cochlespirinae), the radulate terebrids, *Hastula bacillus*, and *Pervicacia tristis* (Pervicaciidae). It is likely, that the turrid species at least have a feeding mechanism similar to that of *F. latisinuata*. The elongation of the anterior oesophagus is usually associated with the permanent shifting of the buccal mass towards the distal end of the proboscis. This is well demonstrated in the Clavatulinae and probably facilitates the eversion of the buccal mass through the mouth.

In all species possessing an elongated oesophagus (except *Pseudomelatoma*), there is a change in the histology of the ante-rior part of the venom gland after its passage through the nerve ring. However, such a change occurs in two species (*Lophiotoma leucotropis* and *Inquisitor* sp.) which lack the elongated oesophagus. The anterior part of the gland is ciliated and duct-like, with no secretory granules. This indicates, that the differentiation of the gland is connected with the elongation of the oesophagus and thus, the latter is a secondary feature.

*Feeding mechanism Type 3*

The majority of Conoidea possess the third type of feeding mechanism, in which separate marginal teeth are used at the proboscis tip for stabbing prey, and the radula not used as a whole organ.

The very specialized radular morphology is the most remarkable and well-known feature of the toxoglossan digestive system. It is characterized by a marked tendency towards a reduction in the strength of the subradular membrane, leading to its complete absence in many species of Turridae, the majority of Terebridae and all Conidae. Species without a subradular membrane, have a radula consisting only of complex, hollow, marginal teeth. They are known for the highly specialized feeding mechanism, in which individual teeth are used at the proboscis tip for stabbing and killing prey with secretions of peptide neurotoxins produced by the venom gland (Oliviera *et al.* 1990).

Despite the similarities with the previous feeding mechanism, those 'higher' conoideans with hollow teeth and no

radular membrane are extremely diverse compared with the 'lower' conoideans. Moreover, this relative diversity has steadily increased throughout the Cenozoic (Sysoev, 1991). This suggests that higher conoideans may possess some adaptive advantages. In our opinion these advantages lie in the features of the morphology of the radular diverticulum.

The higher Conoidea lack a subradular membrane, and the radular diverticulum is divided into two different parts; the radular sac and radular caecum (also known as long and short arms). The caecum serves for the storage of the fully-formed, marginal teeth. Many teeth can be stored; for example, in a specimen of *Mitromorpha (Mitrolumna)* sp. there were 106 teeth in the radular sac compared with 64 in the caecum (Kantor & Sysoev, 1990). Species of higher Conoidea can probably use several teeth in each feeding act. For example, observations on the feeding of *Conus textile* showed that up to 17 teeth can be used in the same attack (Schoenberg, 1981). By contrast, in lower turrids, there is no caecum and probably no more than a single tooth can be used in each feeding act. Predatory attacks by higher Conoidea are thus likely to be more successful, and the mechanism of prey capture probably more efficient. This may explain the relative success of the higher Conoidea.

The feeding and diets of gastropods of this functional type are well known (Oliviera *et al.* 1990) and it is unnecessary to describe the process in detail. Only the most important morphological features should be noted. These are the vestigial, or completely reduced, radular membrane; the absence of an odontophore; the presence of a radular caecum where the fully-formed marginal teeth are stored, and a well-developed oral sphincter for gripping the teeth. The radula is represented by hollow, marginal teeth. The tooth ligament (long flexible stalk attached to the tooth base) is probably the rudiment of the radular membrane (Fig. 23c). Also the gastropods of this group often have enlarged rhynchostomal lips. In some species, the lips are able to invert (i.e. to form an introvert or pseudoproboscis) and this is also used in prey capture. It should be noted, that some vermivorous species of *Conus* (Marsh, 1970) and the fish-feeding *C. geographus* (Johnson & Stablum, 1971) do not stab they prey in every feeding act. This is possibly an initial stage of transition to feeding mechanism type 5.

Usually, teeth are gripped at the proboscis tip by the buccal tube sphincter, but in some turrids the buccal tube introvert (valvule of Sheridan *et al.*, 1973) is involved (Fig. 9). This structure has been reported so far in *Mangelia nebula* (Sheridan *et al.*, 1973; Delaunois & Sheridan, 1989) and in *Eucithara stromboides* (Fig. 10). It is also possible, that the buccal tube introvert can be everted through the mouth opening and have a role in holding the prey.

After envenomation, the prey may be held by the tooth itself, as occurs in many vermivorous species of *Conus* (Kohn, 1959), or with the mouth. The buccal lips may play a role in the transport of prey to the buccal cavity. These are highly protrusive in many Mangeliinae, and at least in *M. nebula* (Fig. 9) can be retracted into the buccal cavity (Delaunois & Sheridan, 1989). A similar possibility was described for *Oenopota* by Bogdanov (1990), who suggested that the buccal lips and the proboscis itself might be inverted into the buccal cavity.

## II. Venom gland absent

### Feeding mechanism Type 4

Gastropods of this group have a radula with a well-developed radular membrane and a proboscis may be either present or reduced. According to the position of the buccal mass they can be divided into two sub-types.

Conoideans of the first sub-type which at present includes only *Strictispira* and probably *Cleospira*, have the buccal mass located at the tip of a well-developed proboscis (Fig. 13). The buccal mass and radular apparatus are large, with two large odontophoral cartilages and massive odontophoral and proboscis retractor muscles. The radula has a strong membrane with two rows of solid, awl-shaped, marginal teeth. The buccal tube is very short and there are no oral sphincters. Apart from the record of polychaete setae in two individuals of *Strictispira paxillus* (Maes, 1983), nothing is known of the habits of this group.

The terminal position of the buccal mass on the muscular proboscis, the short buccal tube and the massive radular apparatus, suggest that when the gastropod is feeding the radula is protracted out of the extended proboscis tip. The solid teeth and absence of venom apparatus suggest that the radula is involved in biting and tearing rather than stabbing. The feeding mechanism is thus probably more similar to other neogastropods such as the Buccinidae rather than to other conoideans.

Conoideans of the second sub-type differ from these of the first one in possessing a basal buccal mass. The radula is well-developed, whilst the proboscis is either absent or highly reduced, and a rhynchostomal introvert is usually present. This feeding mode is found in the Pervicaciidae. The diet of this family is largely unknown, except for *'Terebra' nassoides* which feeds on capitellid polychaetes (Taylor, 1990).

In the Pervicaciidae, the absence of a proboscis means that the rhynchodeal introvert becomes the main organ of prey capture, as occurs in some proboscis-less terebrids such as *T. gouldi* (Miller, 1975). Prey are presumably pulled into the rhynchocoel by the introvert. In *Duplicaria spectabilis* there are large muscular buccal lips and probably a protrusive odontophore (Taylor, 1990, fig. 7). However, in *Pervicacia tristis* and *Duplicaria kieneri* there is a septum with a narrow aperture dividing the rhynchocoel and it is very unlikely that the odontophore can be protruded through the septum. Although we have no direct evidence, it is possible that the septum functions to hold prey during swallowing and perhaps early digestion.

### Feeding mechanism Type 5

Finally, there are many conoideans which lack a radula, venom and salivary glands. Gastropods of this group include some Daphnellinae, Taraninae and some Terebridae. In addition to the absence of foregut glands and radula, a characteristic feature of these species is the very reduced size or complete absence of the proboscis. Radula-less Conoidea either have well-developed, rhynchostomal lips or a large rhynchostomal introvert, as for example, in the Terebridae (Miller, 1975) or *Philbertia linearis* (Sheridan *et al.*, 1973). It is possible, that a rhynchostomal introvert is also present in *Teretiopsis*, although all sectioned specimens have it in the extended position and it was overlooked during the original description (Kantor & Sysoev, 1989). In some turrids, such as

*Cenodagreutes* (Smith, 1967) and *Abyssobela atoxica* (Kantor & Sysoev, 1986), which lack the rhynchodeal introvert, there is a vast rhynchocoel and well-developed cavity between the rhynchodaeum and body walls. The walls of this cavity are connected by numerous transverse muscles. Both the introvert and cavity are lacking in the genus *Taranis* (Taraninae).

A feeding mechanism for radula-less species is known for some terebrids (Miller, 1970, 1975). Thus, *Terebra gouldi* which has a relatively short introvert feeds upon the enteropneust *Ptychodera flava*, and *Terebra maculata* with a long introvert feeds on polychaetes. Prey are caught with the aid of the introvert. Turrids lacking the introvert, but with the cavity between the rhynchodaeum and the body walls, probably engulf prey by contraction of the radial muscles in the wall. This would cause negative pressure and an increase in the inner volume of the rhynchocoel.

The origin of the radula-less feeding mechanism can be easily envisaged. It is known, that in some *Conus* species hypodermic envenomation is not necessary in each feeding attack (Kohn, 1959; Marsh, 1970; Sanders & Wolfson, 1961). It is probable that some Turridae and Terebridae, especially those with well-developed rhynchostomal lips or introvert, also feed without stabbing the prey with radular teeth. Thus, *Daphnella reeveana*, which possesses a venom gland, has a very short proboscis and is probably unable to hold a tooth at its tip (Fig. 4). As stabbing of the prey becomes unnecessary, the proboscis, venom gland and radula disappear. An intermediate stage is found in *Gymnobela emertoni*, in which the proboscis and venom gland have disappeared, but there is still a very short and reduced radular sac, opening to the outer side of the buccal lip (Fig. 8).

# RELATIONSHIPS OF THE CONOIDEA

## Monophyly of the Conoidea

There has been much discussion concerning the relationships of the Conoidea to other prosobranch gastropods; some considering them to be part of a monophyletic group with other neogastropods (Ponder, 1973; Taylor & Morris, 1988), whilst others suggest an origin entirely independent of the neogastropods (Sheridan *et al.* 1973; Shimek & Kohn, 1981; Kantor, 1990).

In this section we briefly review some of the evidence for the relationships of the Conoidea with other prosobranchs. Some of this evidence has been discussed in some detail by Kantor (1990) and only the principal arguments are presented here.

The location of the buccal mass at the base of the proboscis as found in most conoideans, is different from the situation seen in most neogastropods, where the buccal mass is found at the distal end of the proboscis. The proboscis in most conoideans is formed by the elongation of the buccal tube, whilst in neogastropods it originates from the elongation of the anterior oesophagus (Ponder, 1973). However, a basal buccal mass is now known for the neogastropod *Benthobia* (Pseudolividae) which also exhibits a number of other primitive characters, and in *Amalda* (Olividae) (Kantor, 1991). Additionally, in *Benthobia*, the radular retractor muscle passes through the nerve ring and is connected to the columellar muscle (Kantor, 1991 fig. 15a). This condition is seen species of the turrid subfamily Drilliinae, and in most

lower caenogastropods, but is absent in proposciform caenogastropods.

A key autapomorphy of the Conoidea is the possession of the venom apparatus, comprising the venom gland and muscular bulb. There has been much discussion concerning the homology of this gland. But, Ponder (1970; 1973) showed, that in the neogastropod family Marginellidae a long coiled gland, similar in general appearance to the conoidean venom gland is formed by the stripping off of glandular folds from the oesophagus. In some marginellids the gland terminates at the posterior in a muscular bulb which is homologous with the gland of Leiblein. The venom gland of conoideans may have been derived in a similar way and is probably homologous with the glandular folds of the oesophagus and the gland of Leiblein in other neogastropods.

The possession of tubular, accessory salivary glands is also considered to be an apomorphy of the Neogastropoda (Ponder, 1973). These glands are patchily distributed amongst conoideans, but are known in some Turridae, Conidae and Terebridae. Both the histology of the glands (Schultz, 1983; Andrews, 1991) and the position of the opening of the ducts, confirms their homology in the Conoidea and in other neogastropods. The primitive *Benthobia* also has a large accessory salivary gland (Kantor, 1991).

A radula with five teeth in each row, as is found in the turrid subfamily Drilliinae, has been considered as evidence for a separate origin of the Conoidea and Neogastropoda, the latter normally have three or less teeth in each row. (Shimek & Kohn, 1981). However, it is now known that some *Olivella* and Nassariidae have five teeth in each row (Bandel, 1984; Kantor, 1991). All this suggests is that the common ancestor of the Conoidea and the other neogastropods possessed five or more teeth in each row.

In conclusion, conoideans share a number of characters with the neogastropods which suggest a common ancestry. Nevertheless, the evidence both from the position of the buccal mass and the formation of the proboscis, suggests an early divergence of the two groups. An evolutionary scheme for the derivation of the conoidean intraembolic proboscis from the acrembolic type, typical of many mesogastropods, has been developed by Kantor (1990). His arguments corroborate and elaborate Ponder's (1973) hypothesis that the Conoidea diverged from the other neogastropods before the formation of the proboscis. Ontogenetic studies of proboscis and foregut development in the Conoidea and other neogastropods might provide corroborative evidence.

## Relationships within the Conoidea

### Phylogenetic analysis

We attempted to determine relationships within the Conoidea using cladistic analysis of many of the foregut characters described in the first part of this paper, combined with a few shell characters.

### Taxa used

We have included 40 species in the analysis, with at least one from all the currently-recognised, subfamilies. In a few cases we have used previously published work. The species studied represent only a small proportion of living species from any of the subfamilies. Some of these subfamilies are very diverse and morphologically disparate and our sample is certainly

**Table 2.** Characters and character states of the foregut and shell used in cladistic analysis. See text for details of foregut characters. * denotes characters where the states were treated as unordered.

**Foregut characters**

| | | |
|---|---|---|
| 1. | Rhynchodeal introvert | 0 — absent, 1 — present |
| *2. | Rhynchodeal sphincter | 0 — present anterior, 1 — present posterior, 2 — absent |
| 3. | Accessory proboscis structure | 0 — absent, 1 — present |
| 4. | Proboscis | 0 — present, 1 — absent |
| 5. | Transverse muscles in rhynchodeum wall | 0 — absent, 1 — present |
| 6. | Epithelium of posterior rhynchodeal wall continuous with proboscis wall | 0 — absent, 1 — present |
| *7. | Sphincter at distal end of buccal tube | 0 — absent, 1 — one sphincter, 2 — two sphincters |
| 8. | Sphincter in middle of buccal tube | 0 — absent, 1 — present |
| 9. | Sphincter at base of buccal tube | 0 — absent, 1 — present |
| 10. | Buccal tube introvert ('valvule') | 0 — absent, 1 — present |
| 11. | Protrusive lips of buccal tube | 0 — absent, 1 — present |
| 12. | Position of buccal mass | 0 — basal, 1 — distally shifted |
| 13. | Connection of radular retractors to columellar muscle | 0 — present, 1 — absent |
| 14. | Extensible buccal lips | 0 — absent, 1 — present |
| 15. | Septum dividing anterior and posterior areas of the rhynchocoel | 0 — absent, 1 — present |
| 16. | Elongation of oesophagous between buccal mass and nerve ring | 0 — absent, 1 — present |
| 17. | Salivary glands | 0 — two/one glands present, 1 — glands absent |
| 18. | Salivary ducts | 0 — two ducts present, 1 — one duct present |
| 19. | Type of salivary gland | 0 — acinous, 1 — tubular |
| 20. | Accessory salivary glands | 0 — two/one glands present, 1 — glands absent |
| 21. | Radula | 0 — present, 1 — absent |
| 22. | Radular caecum | 0 — absent, 1 — present |
| *23. | Central tooth | 0 — robust muriciform, 1 — narrow 2 — broad with central spine |
| 24. | Lateral teeth | 0 — comb-like, 1 — absent |
| 25. | Marginal teeth | 0 — solid, 1 — wishbone, 2 — hollow, 3 — absent |
| *26. | Type of solid radular teeth | 0 — flat, 1 — curved-pointed, 2 — semi-enrolled (*Hastula bacillus*) |
| *27. | Type of wishbone teeth | 0 — large blade, small accessory limb, 1 — short knife type, equilimbed |
| *28. | Type of hollow teeth | 0 — large base, 1 — thin small base |
| 29. | Venom gland | 0 — present, 1 — present with changed histology in anterior portion, 2 — absent |
| *30. | Connective tissue layer of muscular bulb | 0 — present, 1 — absent |
| *31. | Muscle layers of muscular bulb | 0 — more or less equal, 1 — outer layer thin, 2 — single layer only |
| 32. | Odontophore | 0 — present, 1 — absent |
| 33. | Odontophoral cartilages | 0 — not fused, 1 — fused |

**Shell and opercular characters**

| | | |
|---|---|---|
| *34. | Shell form | 0 — fusiform, 1 — coniform, 2 — turreted, 3 — terebriform, 4 — rounded |
| *35. | Number of protoconch whorls | 0 — less than two, 1 — more than two |
| *36. | Sculpture of the protoconch | 0 — absent or very weak, 1 — present |
| *37. | Siphonal canal | 0 — not differentiated, 1 — moderate, 2 — long |
| *38. | Position of the anal sinus | 0 — sutural, 1 — shoulder, 2 — peripheral, 3 weak or absent |
| 39. | Presence of apertural ornament (teeth on the outer lip) | 0 — absent, 1 — present |
| *40. | Number of the teleoconch whorls | 0 — less than 4, 1 — from 4 to 8, 2 — more than 9 |
| *41. | Development of subsutural ramp | 0 — absent, 1 — present |
| 42. | Operculum | 0 — present, 1 — absent |
| 43. | Position of opercular nucleus | 0 — terminal, 1 — mediolateral |

inadequate. Although anatomical data are available for many terebrids (Taylor, 1990 and unpublished), most of these were eventually excluded from the analysis for the following reason. Many of the morphological trends in the Terebrinae, involve partial to total loss of the foregut organs (Taylor, 1990); thus many of the characters used in the cladistic analysis were recorded as missing. In our earlier attempts at cladistic analysis, terebrid species tended to appear in rather disparate positions on the cladograms. Consequently, we have used only three species to represent the Terebrinae and

Pervicaciinae, the taxa being the least-derived known for each group.

*Characters*

We used 43 characters, coded as 101 states in the analysis. Of these, 35 characters concerned foregut anatomy and a further eight, the shell or operculum. The characters and their states are listed in Table 2. Full discussion of the anatomical characters will be found in the section of this paper concern-

ing foregut anatomy. Additionally, brief descriptions of the shell characters used are given in Appendix 1.

## Outgroup

The relationships of the Conoidea to other Neogastropoda are very unclear and there is no obvious sister group. In our various analyses we used two outgroups. The first is *Benthobia* the most primitive non-coniodean neogastropod known (Kantor, 1991). This gastropod has a buccal mass situated at the base of the proboscis, a muscular connection between the radular retractors and columellar muscles, and a full set of glands connected with the oesophagous. Additionally, we used as a second outgroup a hypothetical ancestral taxon consisting of the underived states, where known, of all the characters used in the analysis.

## Method

The data were analysed using version 3.0 of the PAUP program (Swofford, 1991). Characters 2, 7, 23, 25, 26, 27, 28, 29, 30, 31, 33, 34, 35, 36, 37, 38, 41, 42 were treated as unordered. The matrix of taxa and character states is shown in Table 3.

## Results of phylogenetic analysis

Although we have used many new anatomical characters, the cladistic analysis gave rather disappointing results. The taxa of 'lower conoideans' especially, were rather poorly resolved with major branches supported by rather few weak characters. Additionally, small adjustments to the data set produced rather large changes in tree topography and the number of alternative trees generated.

Despite these limitations we thought it worthwhile to present the results of our analysis, which is the first for the Conoidea to use anatomical characters. Future work will extend on the character set shown in Table 3 and hopefully improve the resolution of the analysis.

A heuristic search with the matrix shown in Table 3 and with Ancestor as outgroup, produced over 900 equally parsimonious trees (189 steps; consistency index = 0.296; homoplasy index 0.704). A 50% majority rule consensus cladogram derived from these trees is shown in Fig. 27. Despite the large number of trees generated, most of the trees are very similar to each other and most of the branches are supported in 75–100% of the trees. Autapomorphies of the internal nodes are listed in Table 4.

The least-derived group are the two species of Drilliidae,

**Table 3.** Matrix of taxa and character states used in the analysis. See Table 2 for further details of characters and caption to Fig. 27 for taxon abbreviations.

| Taxon | Character states |
|---|---|
| Ancestor | 0   0 0 0 ? 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 ? ? ? 0 0 0 0 0 ? 1 ? 1 3 0 ? ? 0 0 |
| Benthobi | 0   1 0 0 0 1 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 ? 1 0 1 ? ? 2 ? ? 0 1 4 0 0 0 3 0 0 0 0 0 |
| PseudomP | 0   0 0 0 0 1 0 0 0 0 0 0 1 0 0 1 0 0 0 1 0 0 0 1 0 1 ? ? 0 0 0 0 4 1 0 1 1 0 1 1 0 0 |
| StrictiP | 0   0 0 0 0 0 0 ? ? 0 0 1 1 0 0 1 0 0 0 1 0 0 ? 1 0 1 ? ? 2 ? ? 0 0 4 0 0 0 1 0 1 1 0 0 |
| ClavusUn | 0   0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 ? ? 0 0 0 0 1 4 0 0 0 1 0 1 1 0 0 |
| SplendrC | 0   0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 ? ? 0 0 0 0 0 4 0 0 0 1 0 1 0 0 0 |
| ClavatuD | 0   2 0 0 0 1 1 0 0 0 0 0 1 0 0 1 0 0 0 1 0 0 2 1 1 ? 1 ? 1 0 0 0 0 1 0 0 0 1 1 0 1 0 1 |
| ClavatuC | 0   0 0 0 0 1 1 0 0 0 0 1 1 0 0 1 1 0 0 1 0 0 2 1 1 ? 1 ? 1 0 0 0 1 0 0 0 1 1 0 2 1 0 1 |
| ClionelS | 0   0 0 0 0 1 2 0 0 0 0 1 1 0 0 1 0 0 0 1 0 0 2 1 1 ? 1 ? 1 0 0 0 1 4 0 0 0 1 0 1 1 0 1 |
| ToxicliT | 0   0 0 0 0 1 0 0 0 0 0 1 1 1 0 1 0 0 0 1 0 0 ? 1 2 ? ? 1 0 0 0 0 4 0 0 1 1 0 1 1 0 1 |
| LophiotL | 0   1 0 0 0 0 1 0 0 0 1 0 1 0 0 0 0 0 0 1 0 0 ? 1 1 ? 1 ? 1 0 0 0 0 0 2 2 0 2 0 0 0 |
| PolystiA | 0   1 0 0 0 0 1 0 0 0 0 ? 0 0 0 0 0 0 0 1 0 0 ? 1 1 ? 1 ? 0 0 0 0 ? 0 0 1 2 2 0 2 0 0 0 |
| TurricuN | 0   0 0 0 0 1 2 0 0 0 1 1 1 1 0 1 0 0 0 1 0 0 2 1 1 ? 1 ? 1 0 0 0 0 0 0 0 0 2 1 0 2 1 0 1 |
| AforiaAb | 0   0 0 0 0 ? 1 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 2 1 1 ? 1 ? 1 0 1 0 0 0 0 0 ? ? 2 1 0 1 0 0 0 |
| FunaLati | 0   1 0 0 0 1 2 0 0 0 1 1 1 0 1 0 0 0 1 0 0 ? 1 1 ? 0 ? 1 0 0 0 1 4 0 0 1 1 0 2 1 0 0 |
| VexitomG | 0   0 0 0 0 1 1 1 0 0 0 1 0 0 1 0 0 0 1 0 0 ? 1 1 ? 0 ? 1 0 0 0 1 4 1 0 1 1 0 1 0 0 0 |
| PilsbryN | 0   0 0 0 0 1 1 0 0 0 0 1 1 1 0 1 0 0 0 1 0 0 ? 1 2 ? ? 1 1 0 0 0 1 4 1 0 0 1 0 1 1 0 0 |
| MicantaP | 0   0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 1 ? 1 2 ? ? 0 0 0 0 1 ? 4 0 0 1 2 0 1 0 0 0 |
| BorsoniO | 0   1 0 0 1 0 1 0 0 0 0 1 0 0 0 0 0 1 0 0 1 ? 1 2 ? ? 1 0 0 0 1 ? 0 0 0 1 1 0 1 1 0 0 |
| TomopleV | 0   2 0 0 0 0 2 0 0 0 0 1 0 0 0 1 ? ? 1 0 1 ? 1 2 ? ? 1 0 0 0 1 ? 4 1 1 0 1 0 2 0 0 0 |
| TropidoF | 0   1 0 0 0 1 0 0 0 0 0 1 1 0 0 0 1 0 1 0 1 ? 1 2 ? ? 0 0 0 0 1 ? 2 0 0 1 1 0 1 1 0 0 |
| OphiodeI | 0   1 0 0 0 0 1 0 0 0 0 1 1 0 0 0 0 0 0 1 ? 1 2 ? ? 1 0 0 1 1 ? 0 0 0 1 1 0 1 0 1 ? |
| AnarithM | 0   1 0 0 0 1 ? ? 0 0 0 0 1 0 0 0 0 ? 0 1 0 1 ? 1 2 ? ? 0 0 0 0 1 ? 4 1 0 0 3 1 0 0 1 ? |
| GlyphosC | 0   1 0 0 0 0 ? ? 0 0 0 1 0 0 0 0 1 0 1 0 1 ? 1 2 ? ? 1 0 0 0 1 ? 4 1 0 1 1 1 1 0 1 ? |
| EucithaS | 0   0 0 0 0 0 0 1 0 1 1 0 1 0 0 0 0 0 1 1 0 1 ? 1 2 ? ? 0 0 0 1 ? 4 1 1 0 1 1 1 1 1 ? |
| MangeliN | 0   0 0 0 0 1 1 0 1 1 1 0 1 1 0 0 0 0 1 1 0 1 ? 1 2 ? ? 0 0 0 1 1 ? 4 1 1 1 1 0 1 0 1 ? |
| MangeliP | 0   0 0 0 0 1 1 0 0 1 1 0 1 1 0 0 0 0 1 1 0 1 ? 1 2 ? ? 0 0 0 1 1 ? 4 1 1 1 1 0 1 0 1 ? |
| OenopotL | 0   1 0 0 0 0 ? 0 0 0 0 0 1 1 0 0 0 0 0 1 0 1 ? 1 2 ? ? 0 0 0 1 1 ? 4 0 1 1 1 0 1 0 0 0 |
| PhilberP | 1   0 0 0 1 0 0 0 0 0 1 0 1 1 1 0 0 0 1 1 0 1 ? 1 2 ? ? 0 0 ? ? 1 ? 4 1 1 1 3 1 1 0 1 ? |
| PhilberL | 1   0 0 0 0 ? ? ? ? 0 0 0 1 1 0 0 1 ? ? 1 1 ? 1 ? 1 ? ? ? ? 2 ? ? 1 ? 4 1 1 1 3 1 1 0 1 ? |
| DaphnelR | 1   0 0 1 0 1 0 0 0 0 0 0 1 1 1 0 0 ? 1 1 1 1 ? 1 2 ? ? 0 0 1 2 1 ? 4 1 1 0 0 1 1 0 1 ? |
| GymnobeE | 1   0 0 1 1 0 ? ? ? 0 0 0 1 1 0 0 0 0 1 1 0 1 ? 1 2 ? ? 0 2 ? ? 1 ? 4 1 1 1 0 0 1 1 1 ? |
| TeretioL | 1   0 0 1 1 0 ? ? ? 0 0 0 1 0 0 0 1 ? ? 1 1 ? ? 1 ? ? ? ? 2 ? ? 1 ? 4 1 1 1 0 0 1 1 ? |
| AbyssobA | 0   0 0 1 1 0 ? ? ? 0 0 0 1 1 0 0 1 ? ? 1 1 ? ? 1 ? ? ? ? 2 ? ? 1 ? 0 ? ? 2 0 0 0 1 1 ? |
| Benthofa | 0   1 0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 1 ? 1 2 ? ? 1 0 0 0 1 ? 0 ? 0 1 0 0 0 1 0 0 0 |
| GenotaNi | 0   0 0 0 0 0 0 1 0 0 0 0 1 ? 0 0 0 0 0 0 1 0 1 ? 1 2 ? ? 1 0 0 0 1 ? 0 1 0 1 1 0 1 1 1 ? |
| ThatcheM | 0   1 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 0 1 1 0 1 ? 1 2 ? ? 0 0 1 2 1 ? 2 1 1 1 0 0 1 0 1 ? |
| TaranisM | 0   2 0 1 0 0 ? ? ? 0 0 0 1 1 0 0 1 ? ? 1 1 ? 1 ? 1 ? ? ? ? 2 ? ? 1 ? 4 0 1 1 0 0 0 1 ? |
| ConusVen | 0   0 0 0 1 0 0 1 0 0 0 1 1 0 0 0 1 0 0 0 1 ? 1 2 ? ? 1 0 0 0 1 ? 1 1 0 0 3 0 1 0 0 0 |
| PervicaT | 1   0 0 1 0 0 ? ? ? 0 0 0 1 1 1 1 0 0 0 1 0 ? ? 1 0 1 ? ? 2 ? ? 0 1 3 0 0 0 3 0 1 0 0 0 |
| HastulaB | 1   0 1 0 1 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 ? 1 0 ? ? ? 0 0 0 0 0 3 1 0 0 3 0 2 0 0 0 |
| DuplicaC | 1   2 1 1 0 0 ? ? ? 0 0 0 1 1 1 0 0 0 0 1 0 0 ? 1 0 1 ? ? 1 ? ? 0 0 3 0 0 0 3 0 2 0 0 0 |

**Table 4.** Synapomorphies for interior nodes. Nodes numbered as in Fig. 27.

| Node | Synapomorphies (Character: state) |
|---|---|
| 1 | 7(1), 20(1), 35(0), 37(0), 38(1) |
| 2 | 13(1), 23(2), 24(1), 26(1) |
| 3 | 1(1), 3(1), 34(3), 38(3), 40(2) |
| 4 | 4(1), 14(1), 15(1), 29(1) |
| 5 | 25(1), 37(1) |
| 6 | 6(1), 16(1), 41(1) |
| 7 | 7(0), 23(0), 25(0) |
| 8 | 12(1) |
| 9 | 33(1), 43(1) |
| 10 | 7(2), 29(1) |
| 11 | 12(1) |
| 12 | 34(0), 40(0) |
| 13 | 14(1), 27(0), 43(0) |
| 14 | 7(1), 35(1) |
| 15 | |
| 16 | 34(0), 37(2) |
| 17 | 2(1), 38(2), 40(2) |
| 18 | 22(1), 25(2), 32(1) |
| 19 | |
| 20 | 20(0) |
| 21 | 2(1), 34(0) |
| 22 | 2(1), 14(1), 28(0) |
| 23 | 18(1) |
| 24 | 14(0), 35(1), 39(1), 42(1) |
| 25 | 7(1), 35(1) |
| 26 | 8(1), 34(0) |
| 27 | 20(0), 39(0) |
| 28 | 19(1), 36(1) |
| 29 | 28(0), 42(1) |
| 30 | 10(1), 11(1) |
| 31 | 6(1), 7(1), 14(1), 31(1) |
| 32 | 30(1), 31(2), 38(0) |
| 33 | 1(1), 14(1), 21(1), 39(1) |
| 34 | 38(3) |
| 35 | 4(1) |
| 36 | 5(1), 29(2), 39(0), 41(1) |
| 37 | 17(1), 40(0) |
| 38 | 1(0), 35(0) |

which are the only conoideans possessing five teeth in each radular row. They also retain the connection of the radular retractor muscle to the columellar muscle. Their distinctive apomorphy is the possession of large, comb-like lateral teeth. We have studied only three species in this group (the third species identical to *Clavus unizonalis*) which are very similar to each other. However, we note the very different hollow, enrolled 'hypodermic-style' marginal teeth of *Imaclava* (Shimek & Kohn, 1981) and the possible 'wishbone' marginals of *Drillia roseola* (McLean, 1971). Anatomical studies of these taxa are needed to determine their status.

All other conoideans are separated from the Drilliidae at Node 2 by the loss of the radular retractor/columellar muscle connection, by the loss of the lateral teeth and possession of curved pointed marginal teeth. None of the non-drilliid taxa that we have included in the cladistic analysis possess lateral teeth, although what appear to be vestigial lateral teeth are seen for example in *Antiplanes* (Kantor & Sysoev, 1991) and a few other species. Also, it is possible that the broad central teeth seen in Cochlespirinae may be formed by fusion of lateral teeth. Another apomorphy at this node is the possession of a broad central tooth with a spine-like central cusp.

Node 3 separates the Terebridae, with five apomorphies including the possession of a rhynchodeal introvert and the accessory proboscis structure. The Pervicaciinae (Node 4) are separated from *Hastula* (representing the Terebrinae) by the loss of the proboscis, the presence of extensible buccal lips, a septum in the rhynchocoel (although this is present in some Terebrinae) and the loss of the venom gland.

Node 5 separates all other conoideans with two apomorphies namely the presence of wishbone marginal teeth and a moderately long siphonal canal. The latter is a weak character and although we consider the fomer to be a strong character, some taxa in Clade 6 have solid teeth which PAUP considers a reversal from the wishbone condition.

Clade 6 comprises taxa with the epithelium of the posterior part of the rhynchodeum continuous with that of the proboscis and with an elongated loop of oesophagus anterior to the nerve ring.

Clade 7 includes two taxa with solid marginal teeth and no buccal tube sphincter and *Toxiclionella* which has hollow teeth. PAUP treats the solid teeth as a reversal, but we think that this is unlikely. However, it is possible that the 'flanges' on the teeth of Strictispirinae may be modifications of a second limb on the tooth. *Toxiclionella* and *Strictispira* are grouped together at Node 8, because both have a buccal mass situated at the distal end of the proboscis. However, *Toxiclionella* shares many characters with the Clavatulinae (including the medio-lateral nucleus of the operculum), but has a very different radula with hollow and barbed marginal teeth firmly attached to the radular ribbon located in the distal buccal mass. Although *Toxiclionella tumida* lacks a central tooth, a clavatuline type central is known in *T. elstoni* (Kilburn, 1985). *Turricula nelliae* (Node 12) shares many apomorphies with clavatuline species and should be transfered from the Cochlespirinae to the Clavatulinae.

PAUP suggests that *Funa* and *Vexitomina* (Crassispirinae) and *Pilsbryspira* (Zonulispirinae) are derived from the Clavatulinae. They share a number of characters, but *Funa* and *Vexitomina* have distinctive wishbone teeth with one broad flat limb and a small, thin, subsidiary limb. *Pilsbryspira* has enrolled marginal teeth and a distal buccal mass. This type of tooth could be derived by enrollment of the crassispirine type of wishbone tooth. Both groups have an operculum with a terminal nucleus which PAUP treats as a reversal from the medio-lateral nucleus of the Clavatulinae.

*Lophiotoma* and *Polystira* (Turrinae) (Node 16) have a peripheral anal sinus and a posteriorly situated rhynchodeal sphincter. *Aforia* has an accessory salivary gland and PAUP treats this appearance as a reversal, the glands having already been lost between the outgroup and the first node. However, it is highly unlikely that these glands are regained once lost. Accessory glands have a very patchy distribution amongst the Conoidea (*Conus*, *Benthofascis* and some Clathurellinae) and apart from their occurrence in some terebrids, *Aforia* is the only 'lower' conoidean in which we have seen the glands. The distribution of this character should become clearer as more species are examined. Maybe significant, is the fact that *Aforia* is the only other conoidean in which the multidigitate osphradial leaflet typical of *Conus* has been found (Sysoev & Kantor, 1988 fig. 2J).

From Node 18 onwards are all the so-called 'higher' conoideans, which in all our analyses form a monophyletic group. The apomorphies which define this node are the presence of a radula caecum for storage of detached radular teeth, hollow, enrolled marginal teeth, loss of the radular
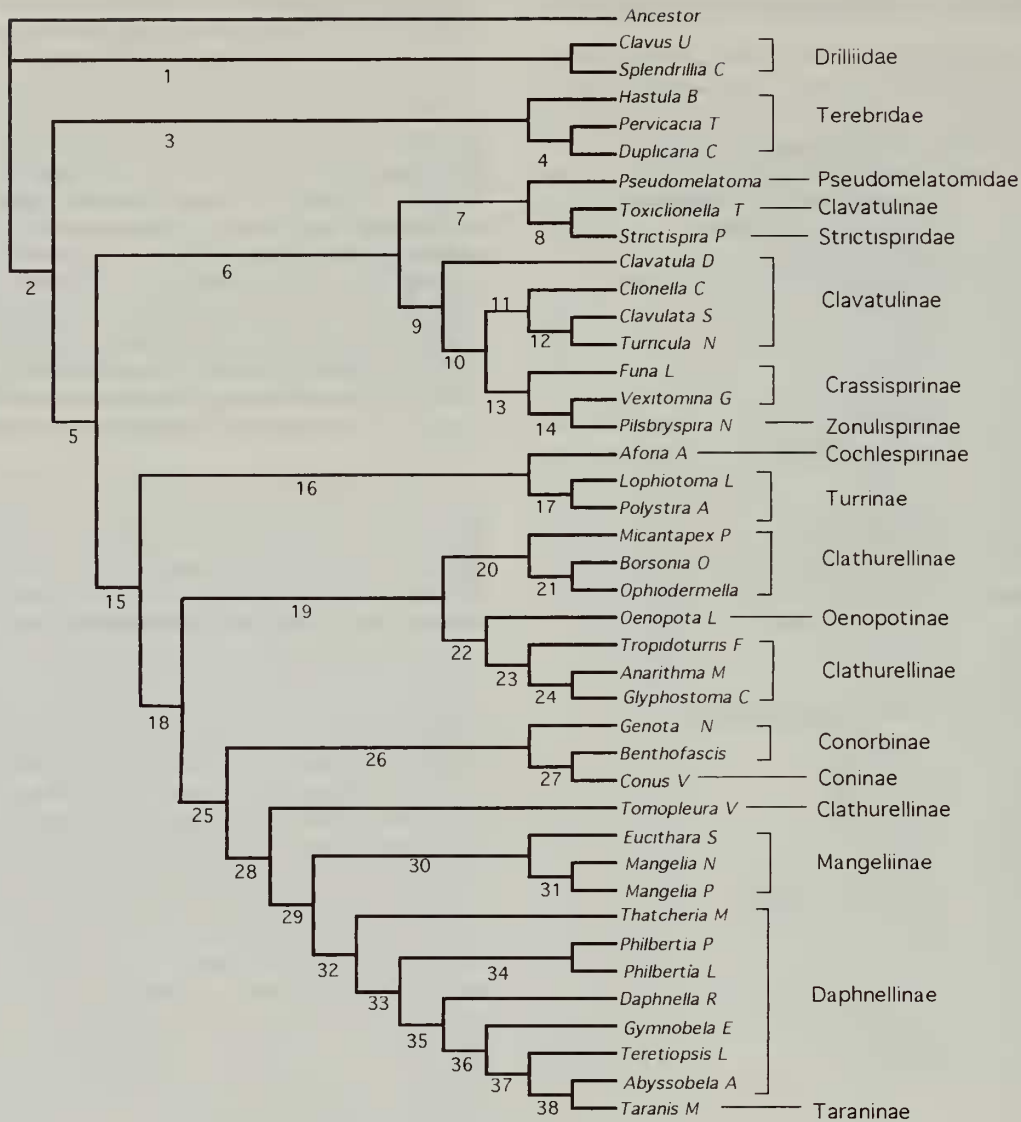
**Fig. 27** Majority-rule (50%) consensus tree. Autapomorphies for each node given in Table 4. Higher taxa names at the top of branches reflect our new classification. Taxon abbreviations in order top to bottom on the tree: Clavus U = *Clavus unizonalis*, Splendrillia C = *Spendrillia chathamensis*, Hastula B =*Hastula bacillus*, Duplicaria C = *Duplicaria colorata*, Pseudomelatoma P = *Pseudomelatoma penicillatus*, Toxiclionella T = *Toxiclionella tumida*, Strictispira P = *Strictispira paxillus*, Clavatula D = *Clavatula diadema*, Clionella S = *Clionella sinuata*, Clavatula C = *Clavatula caerulea*, Turricula N = *Turricula nelliae*, Funa L = *Funa latisinuata*, Vexitomina G = *Vexitomina garrardi*, Pilsbryspira N = *Pilsbryspira nympha*, Aforia A = *Aforia abyssalis*, Lophiotoma L = *Lophiotoma leucotropis*, Polystira A = *Polystira albida*, Micantapex P = *Micantapex parengonius*, Borsonia O = *Borsonia ochraea*, Ophiodermella I = *Ophiodermella inermis*, Oenopota L = *Oenopota levidensis*, Tropidoturris F = *Tropidoturris fossata*, Anarithma M = *Anarithma metula*, Glyphostoma C = *Glyphostoma candida*, Genota N = *Genota nicklesi*, Benthofascis = *Benthofascis biconica*, Conus V = *Conus ventricosus*, Tomopleura V = *Tomopleura reevei*, Eucithara S = *Eucithara stromboides*, Mangelia N = *Mangelia nebula*, Mangelia P = Mangelia powisiana, Thatcheria M = *Thatcheria mirabilis*, Philbertia P = *Philbertia purpurea*, Philbertia L = *Philbertia linearis*, Daphnella R = *Daphnella reeveana*, Gymnobela E = *Gymnobela emertoni*, Teretiopsis L = *Teretiopsis levicarinatus*, Abyssobela A = *Abyssobela atoxica*, Taranis M = *Taranis moerchi*.

ribbon and loss of the odontophore.

Clade 19 is made up of various taxa formerly included in the Borsoniinae and Clathurellinae with the addition of *Oenopota* (Oenopotinae). The apomorphies defining the nodes are very unsatisfactory with many reversals. More characters need to be analysed in these taxa to achieve better resolution.

*Borsonia* and *Ophiodermella* (Node 21) have posteriorly situated rhynchodeal sphincters, and fusiform shells. The

taxa in the other clade (Node 22) have extensible buccal lips and hollow radular teeth with large bases. Although the Oenopotinae have been previously thought to have close affinities with the Mangeliinae, they do have acinous salivary glands, rather than the tubular type associated with the latter subfamily.

A clade comprising *Anarithma* and *Glyphostoma* is defined (Node 24) by three characters; a posteriorly situated rhynchodeal sphincter, a single salivary duct and apertural orna-

ment. *Glyphostoma* has long slender radular teeth and has been separated in the family Clathurellinae (McLean, 1971). *Anarithma* has been classified in the Diptychomitrinae (= Mitrolumninae), but Kilburn (1986) could see no significant differences from the Borsoniinae.

Taxa normally classified in the Borsoniinae (*Ophiodermella*, *Borsonia*, *Tomopleura*, *Micantapex*, *Tropidoturris* and *Anarithma*) do not form a monophyletic group in any of our analyses. For this reason, in the classification derived form this study we are leaving these taxa, along with *Glyphostoma* and others in informal groupings within the subfamily Clathurellinae.

*Benthofascis* (Conorbinae) and *Conus* (Coninae) (Node 27) share a number of characters. They lack an anterior sphincter to the buccal tube, but have have an intermediate sphincter instead. Both have accessory salivary glands and retain an operculum. Additionally, both genera show resorption of the inner shell whorls. Although *Genota* (Node 26) is usually classified in the Conorbinae, it lacks an operculum.

Taxa from Node 28 onwards have tubular salivary glands and most have sculptured protoconchs. The Mangeliinae (Node 30), represented by *Eucithara* and *Mangelia*, are a well-defined group with the distinctive buccal tube introvert, and protrusive lips of the buccal tube. Taxa from Node 32 have a muscular bulb made up of only one muscle layer and lacking the connective tissue layer, with additionally, an anal sinus located at the suture. *Thatcheria* (Node 32) has many characters in common with the Daphnellinae and until many more daphnellines have been examined anatomically it can be classified with them. However a great range of foregut anatomy is found in the Daphnellinae and it may be that the group is paraphyletic. At the extreme end of the tree (Node 36) are taxa which have lost many foregut characters such as radula, proboscis and glands. *Taranis* has been classified in a separate subfamily Taraninae (Kantor & Sysoev, 1989), but it has so few characters that its relationships are obscure. It may be a highly derived daphnelline.

### Conclusions

Our studies have shown that several major autapomorphies associated with the Conoidea have developed independently in separate clades. Also there has been parallel loss of foregut structures. Some of the more important of these are briefly discussed below.

Hollow, enrolled 'hypodermic style' radular teeth are considered a distinctive feature of the conoidean feeding mechanism. Our analysis shows that hollow teeth have been independently derived at least five times in the evolution of the Conoidea. In *Imaclava* the hollow marginal teeth seem to have developed from the enrolling of the flattened drilliinetype of marginal teeth. In *Toxiclionella*, the hollow teeth were derived from wishbone teeth similar to those of *Clavatula* or maybe from solid teeth like those of *Pseudomelatoma*. Hollow teeth are found in many Terebridae and are thought to have been derived from solid teeth via semienrolled intermediate forms such as found in *Hastula bacillus*. The enrolled teeth of *Pilsbryspira* (Zonulispirinae) may have been derived by enrolling of the crassispirine type of wishbone tooth. The hollow teeth of the higher conoideans such Clathurellinae, Coninae, Mangeliinae and Daphnellinae in all their various forms may represent another separate derivation. The radular caecum found in some Terebridae was derived independently of that found in the higher turrids

(Clathurellinae, Oenopotinae, Mangeliinae, Daphnellinae) and Coninae.

The rhynchodeal introvert found in some Daphnellinae, is also found in all Terebridae (including pervicaciines). If our ideas concerning the relationships of the Terebridae are correct, then the structure was evolved independently in the two groups.

A buccal mass situated at the base of the proboscis is considered to be a diagnostic character of the Conoidea (Ponder, 1973). However, in *Turricula nelliae* the buccal mass was shown to be located at the distal end of the proboscis (Taylor, 1985; Miller, 1990). We now know that a distally-shifted buccal mass seems to be common feature of the Clavatulinae and is found also in *Pilsbryspira* (Zonulispirinae) and *Strictispira* (Strictispirinae) which lacks the venom apparatus.

One surprising trend seen in at least four clades is the loss of the venom apparatus. In the Daphnellinae, Taraninae and some Terebrinae this is associated with the loss of the proboscis and radular apparatus. Pervicaciinae have a well developed radula apparatus but no proboscis or venom gland. By contrast, *Strictispira* which also lacks the venom gland, has a proboscis, a distally-located buccal mass and a robust radula apparatus.

## Relationships and status of Terebrinae and Pervicaciinae

Some controversy concerns the status of the Terebrinae and Pervicaciinae. Rudman (1969) and Taylor (1990) suggested an independent origin for the two groups. However, anatomical studies of more species is revealing some shared apomorphies which suggest a common origin.

Although both subfamilies possess elongate multi-whorled shells there are large anatomical differences between the two groups. The family Pervicaciidae was orginally proposed by Rudman (1969) for *Pervicacia tristis*, a terebriform species with no proboscis and venom apparatus, but with an odontophore and a radula with a strong membrane and two sickleshaped, solid teeth in each row. It is now known, that many more 'terebrids' (*Duplicaria* species and others) share these characters and should be included in the family (Taylor, 1990). Other characters of pervicaciids include a rhynchodeal introvert and a septum in some species.

Most of the radulate Terebrinae s.s. possess hollow and barbed, radular teeth, similar to those seen in *Conus* and the Clathurellinae. However, some *Hastula* species possess an odontophore and *Hastula bacillus* has partially-solid teeth (Taylor & Miller, 1989). This discovery demonstrates that the Terebridae must be derived from a lower conoidean with an odontophore and radular ribbon, rather than from some group such as the Clathurellinae, which have lost these structures.

The accessory proboscis structure is an unusual organ found in some Terebrinae, and is known from *Hastula bacillus*, *H. aciculina*, *H. imitatrix*, *H. raphanula*, *Terebra affinis* and *T. pertusa* (Miller 1971, Taylor, 1990; Auffenberg & Lee, 1988; Taylor, unpub.). Some terebrines, for example *Terebra subulata*, also possess a septum dividing the rhynchocoel (Miller, 1971; Taylor 1990). We have found an accessory proboscis structure in the western Australian species *Duplicaria kieneri*, and *Duplicaria colorata* (recently described as a *Hastula* by Bratcher (1988)), which otherwise

have an anatomy similar to *Pervicacia*.

Although the pervicaciines and terebrines apparently differ considerably in foregut anatomy, they share a a number of characters which suggest a common origin (Table 5). The idea that the Terebrinae and Pervicaciinae were derived separately (Rudman, 1969; Taylor, 1990) is rejected. Characters in common between the two groups are: the elongate multi-whorled shell, the rhynchodeal introvert, and in some species the rhynchodeal septum and accessory proboscis structure. Thus, we propose that the common ancestor of the combined Pervicaciinae and Terebrinae clade would have possessed a rhynchodeal introvert, a proboscis, an odontophore, a radula with two solid, sickle-shaped, marginal teeth in each row, a venom gland, a pair of acinous salivary glands, a pair of accessory salivary glands, an accessory proboscis structure and a rhynchodeal septum.

Species in the Pervicaciinae clade have lost the proboscis, venom gland and accessory salivary glands. In the Terebrinae clade, the solid radular teeth were transformed into semi-enrolled and then hollow teeth. The odontophore was also progressively lost. Species with hollow teeth have developed a radular caecum. Other, more-derived terebrines and possibly pervicaciines, have lost virtually all the foregut structures, with the rhynchodeal introvert becoming the main feeding organ (Taylor, 1990).

Because the radula with solid, sickle-shaped marginal teeth and well developed odontophore, is regarded as one of the least-derived for the Conoidea, we regard the Pervicaciinae/Terebrinae clade as an early branch from the rest of the Conoidea. If our hypothesis of relationships is correct, then the hollow, barbed teeth, the radular caecum, the rhynchodeal introvert, and rhynchodeal septum of the terebrids, have been derived independently of those similar structures found in the Daphnellinae and Clathurellinae.

## Status of Conidae

Despite the distinctive shell form and high species diversity of the group, we have little anatomical evidence to support the separation of *Conus* at family-level from other higher turrids. We propose only sub-family status for the group. Every anatomical character-state of the conine foregut is shared with species of Clathurellinae and Conorbinae. Some *Conus* species possess a snout gland in the rhynchocoel, but this

organ has been little studied. *Conus* species also have a distinctive osphradium with the multidigitate leaflets (Taylor & Miller, 1989). However, the detailed structure of the osphradium has been studied in only a few species of Turridae, but at least in some *Aforia* species (Cochlespirinae) there are similar digitate osphradial leaflets (Sysoev & Kantor, 1988). The resorption of the inner shell whorls has been used as a diagnostic character of conines (Kohn, 1990), but the occurrence of this feature has been little studied in other conoideans, although it is present in *Benthofascis* (Conorbinae).

# CLASSIFICATION OF CONOIDEA

## Introduction

Although many of the subfamilial names (as well as apparent synonyms) currently-used within the Turridae were introduced in the 19th or early 20th century, no detailed and well-documented classification was developed in these earlier works. Most authors based their classifications exclusively on shell characters, although Stimpson (1865) used radula data and Fischer (1887) divided the Conoidea into four subfamilies solely by opercular characters. The rather detailed classification of Casey (1904) who recognised eight tribes within the Turridae (Donovaniini are not conoideans), was based on both opercular and shell characters.

Thiele (1931) classified turrids into three subfamilies contained within the family Conidae, with the Terebridae as a separate family. Diagnoses of the turrid subfamilies mainly consisted of combinations of such characters as 'operculate–inoperculate' and 'toxoglossate–nontoxoglossate dentition'. This was the first classification where the taxonomic difference between toxoglossate and nontoxoglossate radulae was definitely indicated. An elaboration of this classification was developed by Wenz (1938) who recognised five subfamilies of Turridae as well as the Conidae and Terebridae.

The classification of Powell (1942, 1966) provided a great stimulus to conoidean taxonomy, and is used, with modifications, by almost all authors concerned with Turridae. Powell recognized nine subfamilies which were based primarily on shell characters, although radular and opercular

**Table 5.**    Comparison of character states between Pervicaciinae and Terebrinae.

| Character | Pervicaciinae | Terebrinae |
|---|---|---|
| Shell shape | Multiwhorled | Multiwhorled |
| Radular teeth | Solid sickle-shaped | If present, usually hollow enrolled marginals |
| Odontophore | Present | Present in some *Hastula* species |
| Radular caecum | Absent | Present in hollow-toothed forms |
| Venom gland | Absent | Present in all with radula & proboscis absent in others |
| Proboscis | Absent | Present in all radulate forms |
| Salivary glands | Present | Present in many species |
| Accessory salivary glands | Absent | Present in some species |
| Rhynchodeal introvert | Present | Present |
| Rhynchodeal septum | Present in some | Present in some |
| Accessory proboscis structure | Present in some | Present in some |
| Eyes | Absent in all? | Present |
| Operculum | Present | Present |

features were also used. Powell believed that the hypodermic toxoglossate dentition could develop independently in different lineages and, more importantly, that the appearance of toxoglossate radula was not a significant reason for separating groups at the subfamilial level. As a result, he classified some taxa having quite different radular types (including both solid and hollow marginal teeth) within a single subfamily.

Morrison (1966) followed Thiele in recognizing a fundamental difference between groups with solid (= nontoxoglossate) and hollow (= toxoglossate) marginal teeth. He suggested a separation at the family level using the families Turridae (with subfamilies Drilliinae, Clavatulinae and 'Lophiotominae or Crassispirinae'), Mangeliidae and 'Pseudomelatominae'.

The subfamily classification of Powell was considerably revised by McLean (1971), who adhered strictly to the principle of grouping together genera with the same type of radula. He also added six subfamilies to Powell's classification; three of these being described as new (Clathurellinae H. & A. Adams, erroneously). Several subfamilies were recognised (or retained after Powell) on shell characters, but which share the same radular type, and some of these seem to be rather poorly documented. However, McLean's classification which includes 15 subfamilies is at present the most detailed and well developed.

In a continuing series of papers concerning South African Turridae, Kilburn (1983, 1985, 1986, 1988), adopted a pragmatic approach (Kilburn, 1983 p.550 ' . . . any practical subdivision is better than none . . . '), and revised to some extent the composition of subfamilies which he studied. He also synonymized the Diptychomitrinae (= Mitrolumninae = Mitromorphinae) with the Borsoniinae.

Bogdanov (1986, 1987, 1990) described a new subfamily Oenopotinae separating the operculate *Oenopota* and its relatives from the Mangeliinae. Additionally, the subfamily Taraninae was recently re-instated (Kantor & Sysoev, 1989).

Some nomenclatural changes in the names and authorships of several subfamilies were made by Cernohorsky (1972, 1985, 1987), and Ponder and Waren (1988).

A different viewpoint was taken by Bouchet and Warén (1980) in their study of North Atlantic deep-sea Turridae. They avoided the use of any subfamilial divisions, considering the present classification of Turridae to be artificial and based mainly on (p. 5) ' . . . more or less randomly selected shell characters'.

At present there is no completely agreed classification of Turridae, nor is there any agreement on which are the taxonomically important characters. The existing variants of turrid classification are based almost exclusively on shell, radular and opercular features.

The Terebridae have similarly been classified mainly on shell characters. H. & A. Adams (1853) and Cossmann (1896) divided the Terebridae into two subfamilies, including the Pusionellinae as the second subfamily. *Pusionella* is now known to belong to the turrid subfamily Clavatulinae. A separate family, the Pervicaciidae, was proposed by Rudman (1969) for *Pervicacia tristis*. However, Bratcher & Cernohorsky (1987) included *Pervicacia* and similar forms in the Terebridae. Taylor (1990) confirmed the distinctiveness of *Pervicacia*, and showed that many other terebrids should be included in the family Pervicaciidae.

The Conidae have long been considered as a fairly homogeneous group, the main problems have concerned the limits

of the family and whether taxa such as *Cryptoconus*, *Conorbis* and *Genota* should be included. Cossmann (1896) for example, included them in the subfamily Conorbinae within the Conidae, whilst Powell (1966) includes this subfamily in the Turridae.

## New classification proposed

As a result of our analysis of foregut characters throughout all the conoidean higher taxa we propose a new classification of the superfamily. This classification represents a rather conservative compromise position. Although in principle the classification should be based upon the results of the phylogenetic analysis, we were constrained by the rather poor resolution obtained with our data set. Moreover, only a rather small subset of conoidean species have been examined in any detail. Information from taxa not included in the cladistic analysis (mainly radular characters) has also been used in constructing the classification. An example of the problem is the family Turridae, which comprises the four subfamilies with wishbone marginal teeth, plus the Zonulispirinae. The cladistic analysis suggests two different clades for these subfamilies. This is certainly possible, but the branches are supported by rather few, and perhaps weak apomorphies. Despite the deficiencies this is the first comprehensive classification of the Conoidea which includes anatomical characters. Below we give descriptions of shell, radula and foregut characters for each of the higher taxa that we recognise. Some of the taxa have only provisional status. For example, the subfamily Clathurellinae has been divided up into five informal groups; it may well be polyphyletic, but we have insufficient evidence to resolve the situation. Similarly, we are uncertain of the status of the Conorbinae and Taraninae.

## Summary of proposed classification

Superfamily Conoidea
    Family Drilliidae (ICZN pending)
    Family Terebridae
        Subfamily    Pervicaciinae
                    Terebrinae
    Family Pseudomelatomidae

    Family Strictispiridae

    Family Turridae
        Subfamily    Clavatulinae
                    Crassispirinae
                    Zonulispirinae
                    Cochlespirinae
                    Turrinae

    Family Conidae
        Subfamily    Clathurellinae
                    Coninae
                    Conorbinae ?
                    Oenopotinae
                    Mangeliinae
                    Daphnellinae
                    Taraninae ?

# DIAGNOSES OF HIGHER TAXA

## Family **Drilliidae** Morrison, 1966 (ICZN pending)

Shell of small to medium size (usually 15–25 mm, up to 50 mm), claviform (with a more or less high spire, and a relatively short, truncated base). Anterior canal indistinct, short or moderately elongate. Anal sinus on the shoulder, rather deep, often sub-tubular when a parietal tubercle is present. Sculpture usually well developed. Protoconch pauci- or multispiral, smooth or, sometimes, carinate (from the second whorl or, rarely, from the beginning). Operculum with terminal nucleus.

RADULA. With strong radular membrane, five teeth in each row, with in some species the complete loss of the central tooth and reduction of the laterals. Rachidian tooth small, with a prominent central cusp and, often, smaller lateral denticles. Lateral teeth are typically broad and curved, comb-like, with many small cusps the outermost being smaller. Marginal teeth have a variable morphology from simple and flat, sometimes with a weak accessory limb, to enrolled. In at least one species (*Imaclava unimaculata*), marginal teeth are hollow and enrolled, whilst the radula as a whole is similar to that of other drilliids.

FOREGUT. Proboscis moderately long, with one or two distal sphincters and sometimes a mid-buccal tube sphincter. Buccal mass at base of proboscis, odontophore well-developed, cartilages either separated or fused. Two acinous salivary glands with two ducts. No accessory salivary glands. Venom gland with uniform histology along its length. Retractor muscle of the radular sac passes through the nerve ring and joins the columellar muscle.

REMARKS. The anatomy and radula are known for only a very few species of Drilliidae. This prevents us from introducing any subfamilial classification of this possibly complex family.

## Family **Terebridae** Mörch, 1852

Elongate, multiwhorled shells, with small quadrate to triangular apertures. Siphonal canal short. Anal sinus not visible. Shell ornament of low axial ribs and grooves, spiral grooves, a few species with tubercles, shells often smooth and polished. Protoconch of 1.5–5 whorls. Operculum rounded with terminal nucleus. Radula with solid sickle-shaped teeth, hollow harpon-like teeth or absent. Rhynchodeal introvert present. Accessory proboscis structure and rhynchodeal septum present in some species. Proboscis present or absent. Odontophore present in some species. Radular caecum present in some. Acinous salivary glands present. Accessory salivary glands present in some species. Venom gland present or absent.

## Subfamily **Pervicaciinae** Rudman, 1969

Shells medium to large, elongate, multiwhorled, anterior canal short, ornament low axial ribs, spiral grooves, often with a subsutural groove. Aperture quadrate. Operculum rounded with terminal nucleus.

RADULA. With strong radula ribbon, two rows of sickle-shaped solid marginal teeth.

FOREGUT. Rhynchodeal introvert. Rhynchodeal septum and accessory proboscis structure present in some species. Proboscis absent. Extensible buccal lips present in some species. Odontophore with two cartilages. Two acinous salivary glands and ducts. Venom gland and accessory salivary glands absent.

## Subfamily **Terebrinae** Mörch, 1852

Shells medium to large, elongate, multiwhorled. Small quadrate to triangular aperture. Short siphonal canal. Shells often smooth and polished. Shell ornament of low axial and spiral ribs and grooves.

RADULA. Where present, long, hollow marginal teeth with narrow bases, barbed or unbarbed. *Hastula bacillus* has semi-enrolled teeth with a distal solid blade. Many species have no radula.

FOREGUT. Rhynchodeal introvert present. Rhynchodeal septum and accessory proboscis structure present in some species. Proboscis long, medium or absent. Odontophore with cartilages present in some *Hastula* species. Radula caecum present in many radulate species. Acinous salivary glands with two ducts usually present. Accessory salivary glands present in some species. Venom gland present or absent in radula-less species.

## Family **Pseudomelatomidae** Morrison, 1966

Shells of medium to large size (35–77 mm), fusiform. Anterior canal moderately elongate. Anal sinus on the shoulder. Protoconch smooth. Operculum with terminal or subcentral nucleus. Egg capsules dome-shaped, with an operculum.

RADULA. With strong radular membrane; three teeth in each radular row. Rachidian is large and rectangular with a large, curved and pointed, central cusp and smaller lateral cusps. Marginal teeth are solid, simple and curved.

FOREGUT. Proboscis very long, no anterior buccal tube sphincter; buccal mass basal or posterior of the proboscis base. Oesophagus elongated between the buccal mass and nerve ring in *Pseudomelatoma*. Odontophore very large with fused cartilages. Acinous salivary glands, paired in *Pseudomelatoma*, but unpaired with a single duct in *Hormospira*. No accessory salivary glands. Venom gland with uniform histology.

## Family **Strictispiridae** McLean, 1971

Shell of rather small size (usually 15–20 mm), claviform. Anterior canal short or indistinct. Sculpture well developed. Deep subtubular sinus is situated on the concave shoulder and bordered with well developed parietal callus. Protoconch smooth, multispiral. Operculum with terminal nucleus.

RADULA. with strong radular membrane; 2 teeth in each row, central and lateral teeth absent (latter maybe diaphanously on optical preparations). Marginal teeth solid, awl-shaped, with pointed tips, a broad base and a mid-tooth flange .

FOREGUT. Proboscis short; buccal mass located near the proboscis tip, odontophore very large and muscular with separate cartilages. Acinous salivary glands small and paired, no accessory salivary gland, no venom apparatus.

REMARKS. This small family possesses unique radular teeth and anatomy, but study of further material is necessary.

## Family **Turridae** H. & A. Adams, 1853

Radula always with a membrane with either 3 radular teeth in a row (central being small or weak), 4 (central lost, laterals diaphanous) or with only marginals. Marginal teeth usually wishbone type, rarely enrolled and hollow. Odontophore always present. Radular sac not subdivided into short and long arms. Venom gland always present. Salivary glands always acinous. Accessory salivary gland either present or absent. Operculum present.

### Subfamily **Clavatulinae** Gray, 1853

Shell medium-sized (usually 15–30 mm, maximum 60 mm), variable in form. Anterior canal moderately long, sometimes short or trun-cated. Whorls usually adpressed below the suture. Anal sinus located on the shoulder slope, rather deep but sometimes indistinct. Protoconch smooth, of 1.5–3 whorls. Axial sculpture predominates or the sculpture is subobsolete and the shell surface is glossy. Operculum ovate, with medio-lateral nucleus. Egg capsules lens-shaped, vertically orientated, without an operculum. Capsules attached to the substratum by a stalk on the edge.

RADULA. Strong radular membrane with 3 to 2 teeth in each row. Central tooth with large, very thin, inconspicuous, basal plate and centrally thickened area with a single cusp. Central tooth sometimes absent (*Toxiclionella s.s.*). Lateral teeth absent. Marginal teeth usually robust wishbone type; hollow harpoon-shaped and barbed in *Toxiclionella*.

FOREGUT. Epithelium of posterior rhynchocoel not glandular and continuous with proboscis. Moderately long proboscis with 1 or 2 anterior buccal tube sphincters. Protrusive lips of the buccal tube may be present (*Turricula*). Buccal mass distal except *Clavatula diadema* in which it is basal but lies within the proboscis. Odontophore medium to small in size, cartilages unfused (except in *Toxiclionella*). Salivary glands acinous, usually paired. Single salivary duct in *Clavatula caerulea*. Single accessory salivary gland in *Toxiclionella*. Anterior venom gland ciliated. Oesophagus elongated between buccal mass and nerve ring.

REMARKS. Some species in this subfamily possess hollow 'toxoglossate' radular teeth associated with strong radular membrane, sometimes, with central teeth. The anatomy and conchological characters of 'toxoglossate' clavatulines are, however, quite similar to those of 'nontoxoglossate' ones. Thus at present we do not consider the appearance of hollow teeth in *Toxiclionella* to be a taxonomic character of subfamilial importance and therefore follow Kilburn (1986) in classifying *Toxiclionella* with other clavatulines.
    The genus *Turricula* Schumacher, 1817 appears very similar to clavatulines in both radular characters and anatomy (the distal buccal mass, ciliated anterior venom gland,

elongated oesophagus between the buccal mass and nerve ring). Moreover, it is also similar to clavatulines in shell characters and in its operculum with mediolateral nucleus. On the other hand, *Turricula* differs in both shell and anatomical characters from those of other 'Turriculinae'. Thus we transfer this genus, as well as *Makiyamaia* which has similar characters, to the subfamily Clavatulinae.

### Subfamily **Crassispirinae** Morrison, 1966

Shell of medium to small size (usually 10–20 mm, sometimes up to 70 mm), claviform to fusiform. Anterior canal usually short. Anal sinus on the whorl shoulder, parietal callus above the sinus often well developed. Spiral and axial sculpture often strong. Protoconch usually paucispiral, initially smooth, later sometimes with axial (rarely spiral) folds. Operculum with terminal nucleus.

RADULA. Strong radular membrane and 4, 3 or 2 teeth in each row. Central tooth when present (*Turridrupa*) is thin, quadrate and unicuspate, lateral teeth usually absent but weak and vestigial in *Crassispira* and *Crassiclava*. Marginal teeth, robust wishbone type or long flat teeth with a slender accessory limb. *Ptychobela* has hollow teeth formed from two components.

FOREGUT. Proboscis moderately long with two anterior buccal tube sphincters. Epithelium of posterior rhynchocoel continuous with proboscis (*Funa latisinuata*). Buccal mass situated at the proboscis base in its contracted state. Odontophore medium to small, with fused cartilages. Salivary glands acinous, fused, ducts paired. Anterior venom gland ciliated in some species. Oesophagus elongated behind buccal mass in some species.

REMARKS. This most large and diverse subfamily of Turridae is defined chiefly on shell and radular characters (i.e. rather small claviform shells with wishbone radular teeth). Data on the anatomy of its representatives are still unsufficient to decide certainly whether the subfamily is of mono- or polyphyletic origin.

### Subfamily **Cochlespirinae** Powell, 1942

Shell of medium to large size (usually 20–40 mm, up to 100 mm), narrow to broadly fusiform or pagodiform. Anterior canal moderately elongate, rarely short or very long. Sculpture variously developed, often with smooth shoulder, and usually with rather short axial ribs below the shoulder, and spiral riblets. Anal sinus usually deep, situated on the shoulder (sometimes on its lower part). Protoconch usually multispiral, smooth or, sometimes, initially smooth and carinated or spirally or axially lirate on subsequent whorls. Operculum with terminal nucleus.

RADULA. Strong radular membrane, with three, four? (see discussion of radula p. 135) or two teeth in each row. Central tooth weak, unicuspid or absent. Marginal teeth of robust wishbone type.

FOREGUT. Proboscis usualy long, with one or two anterior buccal tube sphincters. Buccal mass basal, muscular buccal lips may be present or absent. Odontophore small, cartilages 4, 2 or absent, fused or separate. Salivary glands acinous,

paired or fused. Single accessory salivary gland in *Aforia*.

REMARKS. Since the type-genus of the subfamily Turriculinae, *Turricula* Schumacher, 1817, is transferred to the Clavatulinae (see above), the next available name for this group is Cochlespirinae Powell, 1942.

## Subfamily Zonulispirinae McLean, 1971

Shells rather small (15–25 mm), claviform. Anterior canal usually short, sometimes moderately long. Predominantly spiral sculpture, well developed. Protoconch multispiral, initially with smooth whorls, then with oblique axial riblets. Anal sinus on the shoulder, often sub-tubular, with well developed parietal callus. Operculum with terminal nucleus.

RADULA. With strong membrane and marginal teeth in each row. Teeth semi-enrolled, to rolled, hollow teeth with narrow base. Tips may be barbed or unbarbed.

FOREGUT. Proboscis long, with a single distal buccal tube sphincter. Buccal mass distal. Odontophore small with two unfused cartilages. Buccal lips present. Salivary glands fused. Anterior of venom gland ciliated. Oesophagus elongated between the buccal mass and nerve ring.

## Subfamily Turrinae H. & A. Adams, 1853

Shell usually of medium to large size (up to 110 mm), fusiform. Anterior canal elongated and narrow, rarely truncated. Anal sinus on the whorl periphery. Axial sculpture weak or absent. Protoconch smooth in its initial part, subsequent whorls axially costate; paucispiral protoconchs smooth. Operculum with terminal nucleus. Egg capsules dome-shaped, operculate.

RADULA. Strong radular membrane, 2–3 teeth in each row. Central tooth either well-developed, small or absent, quadrate to rectangular with a strong central cusp. Lateral teeth absent. Marginal teeth of robust wishbone type.

FOREGUT. Proboscis moderately long, rhynchostomal sphincter posterior, a single distal buccal tube sphincter, protrusive lips of buccal tube present. Buccal mass basal. Odontophore small with fused cartilages. Salivary glands paired. No accessory salivary glands. Anterior part of venom gland ciliated.

## Family Conidae Fleming, 1822

Radula consisting of hollow marginal teeth only. Radular membrane absent. Radular diverticulum divided into short and long arms. Odontophore absent. Radula and venom gland may be absent. Salivary glands acinous or tubular. Accessory salivary gland either present or absent. Operculum either present or absent.

## Subfamily Clathurellinae H. & A. Adams, 1858

Shell small to rather large, fusiform to biconic. Anterior canal short or indistinct to moderately elongate. Sculpture predominantly spiral in most genera. Anal sinus deep to very shallow, on the shoulder slope or on the periphery. Columella with or without pleats. Protoconch usually paucispiral, smooth, sometimes carinate or weakly spirally ribbed, rarely axially costate on its last whorl. Operculum with terminal nucleus present, vestigial or absent.

RADULA. Awl- or harpoon-shaped marginal teeth, without (very rarely with) solid base, tooth cavity opens terminally at the proximal end in vast majority of species.

FOREGUT. Proboscis short to long, 1 or 2 anterior buccal tube sphincters, buccal mass basal. Short buccal lips in *Tropidoturris*. Odontophore absent, radular caecum present — divided by septum in *Bathytoma (Micantapex)*. Salivary glands tubular in *Borsonia*, acinous in others, paired, single or absent. Single accessory salivary gland present in some species. Venom gland with uniform histology. No elongation of oesophagus.

REMARKS. This subfamily comprises species classified by other workers in the subfamilies Borsoninae and Clathurellinae. Being very variable in both anatomical and shell characters, the subfamily may be of polyphyletic origin. More species need to be studied anatomically before any satisfactory classification can be attempted. The subfamily is defined mainly by the character of the radular teeth. Several groups of genera can be isolated within Clathurellinae according to shell characters.

'Clathurellid' group is characterized by medium-sized shells (usually 10-25, up to 40 mm), with a moderately elongate siphonal canal, and a well developed, often cancellate sculpture. Columella without pleats, but both inner and outer lips may be denticulated; anal sinus deep located on the shoulder. Protoconch usually multispiral, last whorls with a pronounced medial carination and, sometimes, weak axial lamellae on the lower half. A distinctive feature of this group is densely granulated shell surface of most genera (except of one subgenus of *Glyphostoma* and, probably, *Nannodiella*). Operculum absent. Radular teeth long and slender, slightly curved, without a solid base.

'Bathytomid' group. Shell of medium to rather large size (usually 20–30, up to 70 mm), more or less biconic. Sculpture usually well developed, entirely spiral, ribs often gemmulated by growth lines; typically there is a peripheral tuberculated flange. Anal sinus rather deep, located on the whorl periphery. Columellar pleats strong to obsolete. Protoconch of 1.5–3 whorls, smooth or minutely papillated. Operculum with terminal nucleus. Radular teeth either long, with more or less terminal opening, or short, with large cylindrical solid base and lateral opening.

'Borsoniid' group. Shell of rather small to medium size (usually 15–25, up to 62 mm), fusiform. Anterior canal moderately elongate, sometimes long. Both spiral and axial sculpture may be present. Columellar pleats weak or absent. Anal sinus on the shoulder slope. Protoconch of 1–2 smooth whorls. Operculum fully developed, small or absent. Radular teeth long, without solid base, open terminally, or, rarely, short, with large cylindrical base, open laterally. Egg capsules dome-shaped, with an operculum.

'Mitromorphid' group. Shell small (usually 4–8, up to 17 mm), biconic and 'mitriform'. Anterior canal very short or indistinct. Aperture narrow, columella with or without teeth, outer lip usually denticulated, anal sinus shallow and subsutural. Sculpture predominantly or entirely spiral. Protoconch of 1.5–2 smooth whorls. Operculum absent. Radular teeth

rather short, of 'candle flame' shape, open terminally.

'Tomopleurid' group. Shell rather small to medium sized (6–7 to 37 mm), claviform, with flattened whorls. Anterior canal short. Anal sinus on the shoulder or just below it, moderately deep. Columellar pleats absent. Sculpture entirely spiral (except often raised growth lines), consisting of well developed ribs or heavy keels. Protoconch pauci- or multispiral. In the former case it is smooth or with minute spiral striae or papillae, sometimes carinated; in the latter case first 1–3 whorls with the same sculpture, later ones with axial ribs and, sometimes, minute spiral striae. Operculum with terminal or eccentric nucleus, sometimes absent. Radular teeth short or long and slender, without solid base, open terminally.

## Subfamily **Conorbinae** De Gregorio, 1890

Shell of medium size (up to 40 mm), biconic. Anterior canal short, aperture long and narrow. Sculpture entirely spiral except the growth lines. Anal sinus on the shoulder or almost sutural, relatively deep. Protoconch multispiral, smooth or spirally striated on later whorls. Operculum present or, absent in *Conorbis*.

RADULA. Hollow, marginal teeth with barbed tips and narrow bases (*Conorbis*, Thiele, 192 fig 460; *Benthofascis*, Powell, 1966, fig. 125).

FOREGUT. These observations are based on *Benthofascis*. Rhynchostomal sphincter posteriorly situated. Proboscis moderately long, not folded telescopically as in *Conus*. Distal sphincter of buccal tube absent, intermediate sphincter present. Middle part of buccal tube lined with glandular epithelium. Single acinous salivary gland with two ducts. Single accessory salivary gland. Venom gland with uniform histology, muscular bulb with two muscular layers. No snout gland.

REMARKS. The status of this subfamily is uncertain due to lack of any anatomical information on *Conorbis*. We have excluded *Genota* on the basis of shell morphology and the absence of the operculum.

## Subfamily **Coninae** Fleming, 1822

Shell of medium to large size (usually 30–50 mm, up to more than 120 mm), biconic to conic. The inner shell walls are partially resorbed. Anterior canal short, aperture usually narrow, parallel-sided. Sculpture entirely spiral, usually weak or obsolete, sometimes tubercules on the shoulder. Anal sinus on the upper shoulder or almost sutural, shallow to relatively deep, occupying a rather narrow zone. Protoconch multispiral, smooth or spirally striated. Operculum small, with terminal nucleus, rarely absent. Egg capsules, bilaterally flattened, vasiform, arranged in clusters.

RADULA. Radular teeth harpoon-shaped, barbed or unbarbed on the tips, without solid base, usually open terminally (rarely laterally) at the base.

FOREGUT. Proboscis moderately short and folded in contracted state. Rhynchostome lacks definite sphincter and rhynchodaeum can be greatly expanded to form a rostrum in fish-feeding species. Radial muscles lie in rhynchodeal wall.

Snout gland present in many species. Distal buccal tube sphincter absent, intermediate sphincter present. Middle part of buccal tube is lined with glandular epithelium. Buccal mass basal. Single acinous salivary gland with one or two ducts. Single accessory salivary gland. Venom gland of uniform histology, muscular bulb often with many muscular layers.

## Subfamily **Oenopotinae** Bogdanov, 1987

Shell of small to medium size (usually 10–15, up to 30 mm), oval to fusiform. Anterior canal rather short. Both spiral and axial sculpture well developed. Anal sinus on the shoulder, shallow, and often indistinct. Protoconch paucispiral, predominantly (sometimes entirely) spirally sculptured. Operculum with terminal nucleus present, vestigial, or rarely absent. Egg capsules dome-shaped, with an operculum.

RADULA. Radular teeth with rounded or cylindrical solid base and hollow shaft, sometimes with barbed tip; rarely teeth vestigial; tooth cavity opens laterally between the shaft and the base.

FOREGUT. Proboscis either long, or short and folded in contracted state. Distal sphincter present or absent. Buccal lips large, may be inverted into the buccal cavity. Buccal mass basal. Salivary glands paired, acinous, although shown as tubular (probably erroneously) in *Oenopota levidensis* Shimek (1975). Venom gland of uniform histology. Muscular bulb with a thin outer muscular layer.

REMARKS. Species of this group were previously treated as Mangeliinae, but were isolated as a subfamily primarily on the basis of the presence of an operculum and a spirally sculptured protoconch (Bogdanov, 1987, 1990). None of these features are presently considered as being of subfamilial importance. However, one more character was revealed in our study, the structure of the salivary glands, which distinguished Oenopotinae from the Mangeliinae. We provisionally retain the subfamilial rank of Oenopotinae until the systematic importance of this character becomes certain.

## Subfamily **Mangeliinae** Fischer, 1884

Shell small (usually 5–12 mm, up to 20 mm), ovate to fusiform. Anterior canal rather short. Both spiral and axial sculpture well developed. Anal sinus on the shoulder, shallow to rather deep, sometimes subtubular. Outer lip usually with terminal varix, sometimes denticulate. Protoconch smooth or variously sculptured. Operculum absent. Egg capsules dome-shaped, with an operculum.

RADULA. Radular teeth hollow with a solid base, sometimes with a semi-enrolled shaft; tooth canal opens laterally.

FOREGUT. Proboscis moderately long, with a single or no distal sphincter, intermediate and posterior sphincters sometimes present. Buccal tube introvert ('valvule') present. Distal lips of buccal tube can be inverted. Buccal lips large and can be introverted into the buccal cavity. Buccal mass basal. Salivary glands paired and tubular, accessory salivary glands absent. Venom gland of uniform histology; muscular bulb usually with a thin outer muscle layer.

## Subfamily **Daphnellinae** Deshayes, 1863

Small to moderately large shells (usually 5–15 mm, deep-sea species larger, up to 95 mm). Anal sinus sutural, shaped as a reversed-L, or on the upper shoulder and varying in depth. Sculpture variable, usually cancellate or with predominant spirals, and often with a smooth shoulder. Protoconch usually multispiral, rarely paucispiral, typically diagonally cancellated, although some genera have spiral or axial ribbing. Operculum absent. Egg capsules dome-shaped operculate.

RADULA. Radular teeth with large solid base and barbed or unbarbed tips, tooth cavity opens laterally at the base. Radula absent in some species.

FOREGUT. Rhynchodeal introvert present in many species. Rhynchodeal septum present in some species. Proboscis usually short, often absent. Buccal mass basal. Radula apparatus absent in many species, vestigial in *Gymnobela emertoni*. Radial muscles present in the rhynchodeal wall in radula- and proboscis-less species. Buccal lips well developed, can be intverted into the buccal cavity. Salivary glands paired tubular or absent. Accessory salkivary glands absent. Venom apparatus absent in many species. In *Daphnella reeveana* the anterior part of venom gland is ciliated. Muscular bulb can be single layered.

REMARKS. Although *Thatcheria* is sometimes classified in a separate subfamily Thatcherinae, we failed to find any anatomical or shell characters which would justify separation from the Daphnellinae.

## Subfamily **Taraninae** Casey, 1904

Shell very small (up to 6 mm), ovate-fusiform. Anterior canal rather short. Sculpture well developed. Anal sinus very broad and shallow, situated on the shoulder or immediately below it. Protoconch paucispiral, finely spirally striated, or with spirally aligned granules. Operculum and radula absent.

FOREGUT. Rhynchostomal sphincter absent, no radial muscles in rhynchodeal wall. Proboscis absent. Buccal mass undefined. Salivary glands absent. Venom apparatus absent.

REMARKS. This monotypic radula-less subfamily was reinstated (Kantor & Sysoev, 1989) because it differs in shell characters from any other turrids lacking a radula. However, the very simplified morphology makes the evaluation of the status of the subfamily difficult. For the present we conserve the subfamily, but are unsure of its status.

# APPENDIX 1

## Features of the shell

Shell characters are still important for the systematics of Conoidea, and thus should be included in the analysis. However, there is probably no shell character which is diagnostic of any single group. Moreover, there has been no analysis of the adaptive or evolutionary significance of these shell features. Nevertheless, a few shell characters appear to be useful for the separation of clades.

### Shell shape

This character which is concerned with overall shell shape is the most subjective. We recognise five basic shell shapes: 1, fusiform shell; 2, cone-shaped shell; 3, turreted shell; 4, terebriform shell; 5, a large group of 'intermediate' states, 'biconic-fusiform', 'ovate-biconical', 'ovate-fusiform', 'claviform', etc. characterized by rounded outlines of the shell, which is more or less oval in its general profile.

### Number of protoconch whorls

Two types of protoconch can be recognised; the paucispiral and multispiral. These types of the protoconch were intoduced into turrid systematics by Powell (1942, 1966) and they are widely used in taxonomy. Generally, this subdivision coincides with that between planktotrophic and non-planktotrophic modes of larval development, although there are many exceptions to the rule among turrids (Bouchet, 1990). The character is considered as being of little phylogenetic importance (Bouchet, 1990), but a predominance of a single type of the protoconch can be noted in some taxa. For instance, most Daphnellinae and Conidae have multispiral protoconchs, whilst the paucispiral type is a typical of the Oenopotinae (Bogdanov, 1990). Protoconchs with 1–2 whorls are here considered as paucispiral, and these with two or more whorls as multispiral (Bouchet, 1990).

### Sculpture of the protoconch

The pattern of protoconch sculpture has been widely used in conoidean taxonomy since Powell (1942, 1966). Turrids have a very wide variety of protoconch sculpture and at present, we are unable to classify them into clearly defined types. Thus we recognize only two major states of the character; firstly protoconchs lacking or with only weakly defined sculpture and secondly, protoconchs with well developed sculpture. Some higher taxa may be characterized by the presence or absence of protoconch sculpture. For example, the closely-related *Turricula* and *Clavatula* usually possess a smooth protoconch, whilst in the Turrinae it is usually axially costate. The only type of the protoconch sculpture characteristic of a single subfamily is the 'diagonally cancellated' form found

among species of Daphnellinae, although this is not present in all species.

## Length of siphonal canal

To define groups of shells with different lengths of the anterior siphonal canal we used parameter Rsl (relative siphonal length) of Harasewych (1981). As a result, we recognise three states of the character; a long siphonal canal (Rsl more than 0.39; up to 0.48 in the species studied), moderate canal (Rsl 0.21 to 0.34), short canal (Rsl less than 0.20) or not differentiated from the apertural canal.

## Position of the anal sinus

The anal (labial) sinus is a characteristic feature of Turridae and its position on the shell whorls is widely used for characterizing species and higher taxa (Powell, 1942, 1966; McLean, 1971). We follow Powell (1966) in recognizing 4 types of sinus position; sutural (the deepest point of the sinus is situated near the suture), subsutural (on the whorl shoulder), peripheral, and poorly pronounced (or very slight). Most turrids have a subsutural sinus; a peripheral sinus is characteristic for all Turrinae and some Clathurellinae (*Bathytoma* and related genera); a sutural sinus is common among the Daphnellinae. A weak, almost imperceptible sinus occurs occasionally in many subfamilies. It should be emphasized that sinus types are recognized by growth lines, since the form of sinus at the outer lip of a mature shell may not be the same as that of the immature gastropod.

## Operculum

The presence of an operculum is obviously the primitive state of the character. All 'lower' conoideans have a well developed operculum. Among 'higher' conoideans, the operculum is absent in almost all Daphnellinae and Mangeliinae, but retained in the Oenopotinae and Conidae. In Clathurellinae (incorporating Borsoniinae), the operculum may be present, vestigial or absent, even in apparently closely-related genera (McLean, 1971).

## Position of opercular nucleus

The opercular nucleus is usually situated in a terminal position at the tip of the operculum, but in the Clavatulinae and *Turricula* it is located medio-laterally.

## Presence of apertural armament

The aperture of conoidean shells may be without ornament on the outer lip or columella, or they may bear weak to strong denticles, plications and folds. Armed apertures are found in the subfamilies Mangeliinae, Clathurellinae and Daphnellinae, and mostly amongst tropical shallow-water species.

## Number of teleoconch shell whorls

We recognize three types of shells by this character. 1. shells with a small number of whorls (4 and less); 2. with an intermediate number of whorls (5 to 8); 3. with many whorls (9 and more)

## Presence of well developed subsutural ramp

A subsutural ramp, (a morphologically distinct, often flattened part of the whorl profile immediately below the suture) may be either absent, or pronounced, in many subfamilies of Turridae. Usually, this character is clearly shown by a change in both spiral and axial sculpture in this region of the whorl.

## APPENDIX 2

### Genus-group taxa of recent Turridae S.L. (Compiled by A.V. Sysoev)

The list presented below is of Recent taxa of the genus-group of Turridae s.l. distributed in respect to the classification adopted in the present paper. Since all the data concerning genera described before 1966 were given in Powell's (1966) monograph, type-species and bibliographic citations are included only for genera and subgenera described after 1966. Synonymy is also given only when it differs from that adopted by Powell.

The classification used is to a great extent conservative; we avoid the description of new taxa and radical changes in the existing classification. As a result, some genera are of 'unclear' taxonomic position and cannot be assigned, despite anatomical information, to any existing subfamily (*Toxicochlespira*, for example). Some other genera (such as *Genota*) are only provisionally included into a certain subfamily.

There are 337 valid Recent genera and subgenera.

Family DRILLIIDAE Morrison, 1966. ICZN pending

*Agladrillia* Woodring, 1928
    *Eumetadrillia* Woodring, 1928

*Bellaspira* Conrad, 1868

*Calliclava* McLean, 1971
    Veliger 14(1): 117
    *Cymatosyrinx palmeri* Dall, 1919
*Cerodrillia* Bartsch & Rehder, 1939
    *Lissodrillia* Bartsch & Rehder, 1939
    *Viridrillia* Bartsch, 1943

*Clavus* Montfort, 1810
*Plagiostropha* Melvill, 1927
*Cymatosyrinx* Dall, 1889
*Drillia* Gray, 1838
    *Clathrodrillia* Dall, 1918

*Elaeocyma* Dall, 1918

*Globidrillia* Woodring, 1928

*Horaiclavus* Oyama, 1954
    *Anguloclavus* Shuto, 1983
        Mem. Fac. Sci. Kyushu Univ., ser.D (Geol.) 25(1): 9–10
        *Mangilia multicostata* Schepman, 1913
    *Cytharoclavus* Kuroda & Oyama in Kuroda, Habe & Oyama, 1971
        The sea shells of Sagami Bay: 213
        *Pleurotoma (Mangilia) filicincta* Smith, 1882

*Imaclava* Bartsch, 1944

*Iredalea* Oliver, 1915

*Kylix* Dall, 1919

*Leptadrillia* Woodring, 1928

*Neodrillia* Bartsch, 1943

*Orrmaesia* Kilburn, 1988
   Ann. Natal Mus. 29(1): 201–202
   *Orrmaesia dorsicosta* Kilburn, 1988

*Splendrillia* Hedley, 1922
   *Hauturua* Powell, 1942

*Spirotropis* G.O.Sars, 1878

*Syntomodrillia* Woodring, 1928

*Tylotiella* Habe, 1958

?*Acinodrillia* Kilburn, 1988
   Ann. Natal Mus. 29(1): 223
   *Acinodrillia viscum* Kilburn, 1988 (s.d. Kilburn, 1988,
   Ann. Natal Mus. 29(2): 557)

?*Douglassia* Bartsch, 1934

?*Fenimorea* Bartsch, 1934

?*Paracuneus* Laseron, 1954

Family PSEUDOMELATOMIDAE Morrison, 1966

*Hormospira* Berry, 1958
*Pseudomelatoma* Dall, 1918
   (=*Laevitectum* Dall, 1919)

*Tiariturris* Berry, 1958

Family STRICTISPIRINAE McLean, 1971

*Cleospira* McLean, 1971
   Veliger 14(1): 125
   *Monilispira ochsneri* Hertlein & Strong, 1949
*Strictispira* McLean, 1971
   Veliger 14(1): 125
   *Crassispira ericana* Hertlein & Strong, 1951

Family TURRIDAE H. & A.Adams, 1853

Subfamily CLAVATULINAE Gray, 1853

*Benthoclionella* Kilburn, 1974
   Ann. Natal Mus. 22(1): 214
   *Benthoclionella jenneri* Kilburn, 1974

*Clavatula* Lamarck, 1801

*Clionella* Gray, 1847

*Makiyamaia* Kuroda in MacNeil, 1960

*Perrona* Schumacher, 1817

*Pusionella* Gray, 1847

*Scaevatula* Gofas, 1989
   Arch. Molluskenk. 120(1/3): 16
   *Scaevatula pelisserpentis* Gofas, 1989
*Toxiclionella* Powell, 1966
   *Caliendrula* Kilburn, 1985
   Ann. Natal Mus. 26(2): 442–443
   *Latiaxis? elstoni* Barnard, 1962

*Turricula* Schumacher, 1817

?*Makiyamaia* Kuroda in MacNeil, 1960

Subfamily CRASSISPIRINAE Morrison, 1966

*Aoteadrillia* Powell, 1942

*Austrodrillia* Hedley, 1918
   *Regidrillia* Powell, 1942

*Belalora* Powell, 1951

*Buchema* Corea, 1934

*Calcatodrillia* Kilburn, 1988
   Ann. Natal Mus. 29(1): 290–291
   *Calcatodrillia chamaeleon* Kilburn, 1988

*Carinodrillia* Dall, 1919

*Carinapex* Dall, 1924

*Ceritoturris* Dall, 1924

*Conorbela* Powell, 1951

*Conticosta* Laseron, 1954

*Crassiclava* McLean, 1971
   Veliger 14(1): 121
   *Pleurotoma turricula* Sowerby, 1834

*Crassispira* Swainson, 1840
   *Burchia* Bartsch, 1944
   *Crassispirella* Bartsch & Rehder, 1939
   *Dallspira* Bartsch, 1950
   *Gibbaspira* McLean, 1971
      Veliger 14(1): 122
      *Pleurotoma rudis* Sowerby, 1834
   *Glossispira* McLean, 1971
      Veliger 14(1): 121
      *Pleurotoma harfordiana* Reeve, 1843
   *Monilispira* Bartsch & Rehder, 1939
   *Striospira* Bartsch, 1950
   (= *Adanaclava* Bartsch, 1950)

*Doxospira* McLean, 1971
   Veliger 14(1): 124
   *Doxospira hertleini* Shasky, 1971

*Epideira* Hedley, 1918
   (=*Epidirona* Iredale, 1931)

*Funa* Kilburn, 1988
   Ann. Natal Mus. 29(1): 267–268
   *Drillia laterculoides* Barnard, 1958

*Haedropleura* Bucquoy, Dautzenberg & Dollfus, 1883

*Hindsiclava* Hertlein & Strong, 1955
   (= *Turrigemma* Berry, 1958)

*Inodrillia* Bartsch, 1943

*Inquisitor* Hedley, 1918

*Kurilohadalia* Sysoev & Kantor, 1986
   Zoologicheskij Zhurnal 65(10): 1462–1463
   *Kurilohadalia elongata* Sysoev & Kantor, 1986

*Lioglyphostoma* Woodring, 1928

*Maesiella* McLean, 1971
   Veliger 14(1): 123
   *Maesiella maesae* McLean & Poorman, 1971

*Mauidrillia* Powell, 1942

*Miraclathurella* Woodring, 1928

*Naskia* Sysoev & Ivanov, 1985
   Zoologicheskij zhurnal 64(2): 196–197
   *Naskia axiplicata* Sysoev & Ivanov, 1985

*Naudedrillia* Kilburn, 1988
   Ann. Natal Mus. 29(1): 276–278
   *Naudedrillia nealyoungi* Kilburn, 1988

*Nquma* Kilburn, 1988

Ann. Natal Mus. 29(1): 247
*Pleurotoma rousi* Sowerby, 1886

*Plicisyrinx* Sysoev & Kantor, 1986
Zoologicheskij Zhurnal 65(10): 1465–1466
*Plicisyrinx decapitata* Sysoev & Kantor, 1986

*Psittacodrillia* Kilburn, 1988
Ann. Natal Mus.: 29(1): 253
*Pleurotoma bairstowi* Sowerby, 1886

*Ptychobela* Thiele, 1925

*Turridrupa* Hedley, 1922

*?Paradrillia* Makiyama, 1940
(= *Iwaoa* Kuroda, 1953)
(= *Vexitomina* Powell, 1942)
*Coronacomitas* Shuto, 1983
Mem. Fac. Sci. Kyushu Univ., ser.D (Geol.) 25(1): 1–2
*Paradrillia (Coronacomitas) gemmata* Shuto, 1983

*?Pseudexomilus* Powell, 1944

Subfamily ZONULISPIRINAE McLean, 1971

*Compsodrillia* Woodring, 1928
*Mammillaedrillia* Kuroda & Oyama in Kuroda, Habe & Oyama, 1971
The sea shells of Sagami Bay: 208
*Compsodrillia (Mammillaedrillia) mammillata*
Kuroda & Oyama in Kuroda, Habe & Oyama, 1971

*Pilsbryspira* Bartsch, 1950
*Nymphispira* McLean, 1971
Veliger 14(1): 126
*Crassispira nymphia* Pilsbry & Lowe, 1932

*Zonulispira* Bartsch, 1950

Subfamily COCHLESPIRINAE Powell, 1942

*Abyssocomitas* Sysoev & Kantor, 1986
Zoologicheskij Zhurnal 65(10): 1461–1462
*Abyssocomitas kurilokamchatica* Sysoev & Kantor, 1986

*Aforia* Dall, 1889
*Abyssaforia* Sysoev & Kantor, 1987
Veliger 30(2): 117
*Aforia (Abyssaforia) abyssalis* Sysoev & Kantor, 1987
*Dallaforia* Sysoev & Kantor, 1987
Veliger 30(2): 115–116
*Irenosyrinx? crebristriata* Dall, 1908
*Steiraxis* Dall, 1895

*Anticomitas* Powell, 1942

*Antimelatoma* Powell, 1942

*Antiplanes* Dall, 1902
(= *Rectiplanes* Bartsch, 1944)

*Apiotoma* Cossmann, 1889

*Carinoturris* Bartsch, 1944

*Clavosurcula* Schepman, 1913

*Cochlespira* Conrad, 1865
(=*Ancistrosyrinx* Dall, 1881)
(=*Pagodosyrinx* Shuto, 1969
Mem. Fac. Sci. Kyushu Univ., ser.D (Geol.) 19(1): 190–191
*Pleurotoma (Ancistrosyrinx) travancorica granulata* Smith,1904)

*Comitas* Finlay, 1926

*Fusiturricula* Woodring, 1928
*Fusisyrinx* Bartsch, 1934

*Knefastia* Dall, 1919

*Leucosyrinx* Dall, 1889
*Sibogasyrinx* Powell, 1969
Indo-Pacific Moll. 2(10): 343
*Surcula pyramidalis* Schepman, 1913

*Marshallena* Allan, 1927

*Megasurcula* Casey, 1904

*Nihonia* MacNeil, 1960

*Paracomitas* Powell, 1942

*Parasyrinx* Finlay, 1924
*Lirasyrinx* Powell, 1942

*Pyrgospira* McLean, 1971
Veliger 14(1): 119
*Pleurotoma obeliscus* Reeve, 1843

*Rhodopetoma* Bartsch, 1944

*Schepmania* Shuto, 1970 Venus 29(2): 37–38 *Surcula variabilis* Schepman, 1913

*?Micropleurotoma* Thiele, 1929

Subfamily TURRINAE H. & A.Adams, 1853 (1840)

*Cryptogemma* Dall, 1918

*Decollidrillia* Habe & Ito, 1965

*Epidirella* Iredale, 1931

*Fusiturris* Thiele, 1929

*Gemmula* Weinkauff, 1875
*Pinguigemmula* MacNeil, 1960
*Ptychosyrinx* Thiele, 1925

*Lophiotoma* Casey, 1904
(= *Lophioturris* Powell, 1964)
*Unedogemmula* MacNeil, 1960
*Xenuroturris* Iredale, 1929

*Lucerapex* Iredale, 1936

*Polystira* Woodring, 1928

*Turris* Roeding, 1798
*Annulaturris* Powell, 1966

Family CONIDAE Fleming, 1822

Subfamily CLATHURELLINAE H. & A.Adams, 1858

'bathytomid' group of genera

*Bathytoma* Harris & Burrows, 1891
*Micantapex* Iredale, 1936
*Parabathytoma* Shuto, 1961
*Riuguhdrillia* Oyama, 1951

*Paraborsonia* Pilsbry, 1922

'borsoniid' group of genera

*Asthenotoma* Harris & Burrows, 1891

*Borsonella* Dall, 1908
*Borsonellopsis* McLean, 1971
The Veliger 14(1): 126–127
*Leucosyrinx erosina* Dall, 1908
*Borsonia* Bellardi, 1839
*Boettgeriola* Wenz, 1943

*Cordieria* Rouault, 1848

*Cruziturricula* Marks, 1951

*Ophiodermella* Bartsch, 1944

*Tropidoturris* Kilburn, 1986
        Ann. Natal Mus. 27(2): 645–646
        *Pleurotoma scitecostata* Sowerby, 1903

*Typhlomangelia* G.O.Sars, 1878

*Typhlosyrinx* Thiele, 1925

?*Darbya* Bartsch, 1934

'clathurellid' group of genera

*Clathurella* Carpenter, 1857

*Comarmondia* Monterosato, 1884

*Corinnaeturris* Bouchet & Waren, 1980
        J. Moll. Stud., suppl.8: 77
        *Pleurotoma leucomata* Dall, 1881

*Crockerella* Hertlein & Strong, 1951

*Glyphostoma* Gabb, 1872
        *Glyphostomopsis* Bartsch, 1934
        *Euglyphostoma* Woodring, 1970
            Prof. pap. U.S. Geol. Survey 306–D: 401
            *Glyphostoma partefilosa* Dall, 1919

*Nannodiella* Dall, 1919

*Strombinoturris* Hertlein & Strong, 1951

?*Etrema* Hedley, 1918
        *Etremopa* Oyama, 1953
        *Etremopsis* Powell, 1942

?*Genota* H. & A.Adams, 1853

'mitromorphid' group of genera

*Anarithma* Iredale, 1916

*Arielia* Shasky, 1961
        *Vexiariella* Shuto, 1983
            Mem. Fac. Sci. Kyushu Univ., ser.D (Geol.) 25(1): 6
            *Ariella (Vexiariella) cancellata* Shuto, 1983

*Diptychophlia* Berry, 1964

*Lovellona* Iredale, 1917

*Maorimorpha* Powell, 1939

*Mitrellatoma* Powell, 1942

*Mitromorpha* Carpenter, 1865
        *Mitrolumna* Bucquoy, Dautzenberg & Dollfus, 1883
        (=*Apaturris* Iredale, 1917)
        (=*Cymakra* Gardner, 1937)
        (= *Helenella* Casey, 1904)
        (= *Itia* Marwick, 1931)
        (= *Mitrihara* Hedley, 1922)

*Scrinium* Hedley, 1922

*Zetekia* Dall, 1918

'tomopleurid' group of genera

*Drilliola* Cossmann, 1903

*Microdrillia* Casey, 1903
        (= *Acropota* Nordsieck, 1977, nom.nov. pro *Acrobela* Thiele, 1925
            non Foerster, 1862
            The Turridae of the European seas: 59)

*Phenatoma* Finlay, 1924

*Pulsarella* Laseron, 1954

*Suavodrillia* Dall, 1918

*Tomopleura* Casey, 1904
    *Maoritomella* Powell, 1942

?*Austroturris* Laseron, 1954

?*Filodrillia* Hedley, 1922

?*Heteroturris* Powell, 1967
        Indo-Pacific Moll. 1(7): 411
        *Heteroturris sola* Powell, 1967

Subfamily? CONORBIINAE De Gregorio, 1890

*Conorbis* Swainson, 1840

*Benthofascis* Iredale, 1936

Subfamily OENOPOTINAE Bogdanov, 1987

*Curtitoma* Bartsch, 1941
    (= *Widalli* Bogdanov, 1986
        Zoologicheskij Zhurnal 65(1): 45
        *Pleurotoma trevelliana* Turton, 1834)

*Granotoma* Bartsch, 1941

*Obesotoma* Bartsch, 1941

*Oenopota* Mörch, 1852
        *Nodotoma* Bartsch, 1941

*Oenopotella* Sysoev, 1988
        Zoologicheskij zhurnal 67(8): 1119–1120
        *Oenopotella ultraabyssalis* Sysoev, 1988

*Propebela* Iredale, 1918
        *Canetoma* Bartsch, 1941
        (=*Funitoma* Bartsch, 1941)

?*Lorabela* Powell, 1951

Subfamily MANGELIINAE Fischer, 1883

*Acmaturris* Woodring, 1928

*Agathotoma* Cossmann, 1899

*Anacithara* Hedley, 1922

*Antiguraleus* Powell, 1942

*Apispiralia* Laseron, 1954

*Apitua* Laseron, 1954

*Bactrocythara* Woodring, 1928

*Bela* Gray, 1847

*Belaturricula* Powell, 1951

*Bellacythara* McLean, 1971
        The Veliger 14(1): 128
        *Clavatula bella* Hinds, 1843

*Benthomangelia* Thiele, 1925

*Brachycythara* Woodring, 1928

*Cacodaphnella* Pilsbry & Lowe, 1932

*Citharomangelia* Kilburn, 1992
        Annals Natal Mus. 33(2): 508–9
        *Mangilia africana* Sowerby, 1903

*Clathromangelia* Monterosato, 1884

*Cryoturris* Woodring, 1928

*Cytharella* Monterosato, 1875
  *Cyrtocythara* Nordsieck, 1977
    The Turridae of European seas: 34
    *Pleurotoma albida* Deshayes, 1834
  *Rugocythara* Nordsieck, 1977
    The Turridae of European seas: 35
    *Pleurotoma rugulosa* Philippi, 1844

*Eucithara* Fischer, 1883

*Euclathurella* Woodring, 1928

*Fehria* van Aartsen, 1988
    La Conchiglia 20(232–233): 232
    *Ginnania taprurensis* Pallary, 1904

*Gingicithara* Kilburn, 1992
    Annals Natal Mus. 33(2): 495–6
    *Mangelia lyrica* Reeve, 1846

*Glyphoturris* Woodring, 1928

*Glyptaesopus* Pilsbry & Olsson, 1941

*Guraleus* Hedley, 1918
  *Euguraleus* Cotton, 1947
  *Mitraguraleus* Laseron, 1954

*Heterocithara* Hedley, 1922

*Ithycythara* Woodring, 1928

*Kurtzia* Bartsch, 1944

*Kurtziella* Dall, 1918
  *Granoturris* Fargo, 1953
  *Rubellatoma* Bartsch & Rehder, 1939
  *Kurtzina* Bartsch, 1944

*Leiocithara* Hedley, 1922

*Lienardia* Jousseaume, 1884
  *Acrista* Hedley, 1922
  *Hemilienardia* Boettger, 1895
  *Thetidos* Hedley, 1899

*Liracraea* Odhner, 1924

*Macteola* Hedley, 1918

*Mangelia* Risso, 1826

*Mangiliella* Bucquoy, Dautzenberg & Dollfus, 1883
  *Lyromangelia* Monterosato, 1917

*Marita* Hedley, 1922

*Neoguraleus* Powell, 1939

*Notocytharella* Hertlein & Strong, 1955

*Papillocithara* Kilburn, 1993
    Annals Natal Mus. 33(2): 516–7
    *Papillocithara hebes* KIlburn, 1992

*Paramontana* Laseron, 1954

*Platycythara* Woodring, 1928

*Pseudoetrema* Oyama, 1953

*Pseudoraphitoma* Boettger, 1895

*Pyrgocythara* Woodring, 1928

*Saccharoturris* Woodring, 1928

*Stellatoma* Bartsch & Rehder, 1939

*Tenaturris* Woodring, 1928

*Thelecythara* Woodring, 1928

*Turrella* Laseron, 1954

*Vitjazinella* Sysoev, 1988
    Zoologicheskij zhurnal 67(8): 1122
    *Vitjazinella multicostata* Sysoev, 1988

*Vitricythara* Fargo, 1953

?*Anticlinura* Thiele, 1934

?*Conopleura* Hinds, 1844

?*Hemicythara* Kuroda & Oyama in Kuroda, Habe & Oyama, 1971
    The sea shells of Sagami Bay: 229
    *Pleurotoma octangulata* Dunker, 1860

?*Paraclathurella* Boettger, 1895

Subfamily DAPHNELLINAE Deshayes, 1863

*Abyssobela* Kantor & Sysoev, 1986
    Zoologicheskij Zhurnal 65(4): 492
    *Abyssobela atoxica* Kantor & Sysoev, 1986

*Antimitra* Iredale, 1917

*Asperdaphne* Hedley, 1922
  *Aspertilla* Powell, 1944

*Austrodaphnella* Laseron, 1954

*Bathybela* Kobelt, 1905
  (= *Bathypota* Nordsieck, 1968
    The Turridae of European seas: 28
    *Pleurotoma tenellula* [sic] Locard, 1897)

*Buccinaria* Kittl, 1887

*Cryptodaphne* Powell, 1942
  *Acamptodaphne* Shuto, 1971
    Venus 30(1): 10
    *Pleurotomella biconica* Schepman, 1913

*Cenodagreutes* Smith, 1967
    The Veliger 10(1): 1
    *Cenodagreutes aethus* Smith, 1967

*Daphnella* Hinds, 1844
  *Diaugasma* Melvill, 1917
  *Hemidaphne* Hedley, 1918

*Eubela* Dall, 1889

*Eucyclotoma* Boettger, 1895

*Exomilus* Hedley, 1918

*Famelica* Bouchet & Waren, 1980
    J. Moll. Stud., suppl.8: 88
    *Pleurotomella catharinae* Verrill & Smith, 1884

*Fusidaphne* Laseron, 1954

*Gymnobela* Verrill, 1884
  (= *Majox* Nordsieck, 1968
    Die europaischen Meeres-Gehause Schnecken: 182
    *Pleurotomella bairdi* Verrill & Smith, 1884)
  (= *Watsonaria* Nordsieck, 1968 (nomen nudum)
    Die europaischen Meeres-Gehause Schnecken: 182
    *Clathurella watsoni* Dautzenberg, 1889)
  *Theta* Clarke, 1959

*Isodaphne* Laseron, 1954

*Kermia* Oliver, 1915

*Kuroshiodaphne* Shuto, 1965

*Lusitanops* Nordsieck, 1968
  Die europaischen Meeres-Gehause schnecken: 181
  *Pleurotomella lusitanica* Sykes, 1906
  (= *Pseudazorita* Nordsieck, 1977 (published as nomen nudum)
  The Turridae of the European seas: 31 (published as
  a subgenus of *Thesbia*)
  *Pleurotoma blanchardi* Dautzenberg & Fischer, 1896,
  s.d. Bouchet, Waren, 1980, 1980, J. Moll. Stud.,
  suppl. 8: 83)

*Magnella* Dittmer, 1960

*Microdaphne* McLean, 1971
  The Veliger 14(1): 129–130
  *Philbertia trichodes* Dall, 1910

*Microgenia* Laseron, 1954

*Neopleurotomoides* Shuto, 1971
  Venus 30(1): 5–6
  *Clathurella rufoapicata* Schepman, 1913

*Nepotilla* Hedley, 1918

*Ootomella* Bartsch, 1933

*Pagodidaphne* Shuto, 1983
  Mem. Fac. Sci. Kyushu Univ., ser.D (Geol.) 25(1): 21
  *Pagodidaphne colmani* Shuto, 1983

*Philbertia* Monterosato, 1884
  (= *Lineotoma* Nordsieck, 1977, nom.nov. pro *Cirillia*
  Monterosato, 1884 non Rondani, 1856
  The Turridae of the European seas: 18)
  *Glyphostomoides* Shuto, 1983
  Mem. Fac. Sci. Kyushu Univ., ser.D (Geol.) 25(1): 16–17
  *Philbertia (Glyphostomoides) queenslandica* Shuto, 1983

*Phymorhynchus* Dall, 1908

*Pleurotomella* Verrill, 1873
  (= *Azorilla* Nordsieck, 1968
  Die europaischen Meeres-Gehause Schnecken: 184
  *Pleurotoma megalembryon* Dautzenberg & Fischer, 1896)
  (= *Azorita* Nordsieck, 1968
  Die europaischen Meeres-Gehause Schnecken: 184–185
  *Pleurotoma bureaui* Dautzenberg & Fischer, 1897)
  *Anomalotomella* Powell, 1966

*Pontiothauma* Smith, 1895

*Pseudodaphnella* Boettger, 1895

*Raphitoma* Bellardi, 1848
  *Cyrtoides* Nordsieck, 1968
  Die europaischen Meeres-Gehause schnecken: 176
  *Raphitoma rudis* Scacchi, 1836 (= *R. (C.) neapolitana* Nords-
  ieck, 1977, nom.nov. pro *R. rudis* Scacchi, 1836 non Broderip)

*Rimosodaphnella* Cossmann, 1915

*Spergo* Dall, 1895
  *Speoides* Kuroda & Habe, 1961

*Stilla* Finlay, 1926

*Tasmadaphne* Laseron, 1954

*Teretia* Norman, 1888

*Teretiopsis* Kantor & Sysoev, 1989
  J.Moll.Stud. 55: 538
  *Teretiopsis levicarinatus* Kantor & Sysoev, 1989

*Thatcheria* Angas, 1877

*Tritonoturris* Dall, 1924

*Truncadaphne* McLean, 1971
  The Veliger 14(1): 129
  '*Philbertia*' *stonei* Hertlein & Strong, 1939

*Tuskaroria* Sysoev, 1988
  Zoologicheskij Zhurnal 67(7): 970–972
  *Tuskaroria ultraabyssalis* Sysoev, 1988

*Veprecula* Melvill, 1917

*Vepridaphne* Shuto, 1983
  Mem. Fac. Sci. Kyushu Univ., ser.D (Geol.) 25(1): 17
  *Daphnella cestrum* Hedley, 1922

*Xanthodaphne* Powell, 1942

*Zenepos* Finlay, 1928

?*Aliceia* Dautzenberg & Fischer, 1897

?*Benthodaphne* Oyama, 1962

?*Otitoma* Jousseaume, 1898

?*Thesbia* Jeffreys, 1867

Subfamily? TARANINAE Casey, 1904

*Taranis* Jeffreys, 1870

CONIDAE INCERTAE SEDIS

*Austrocarina* Laseron, 1954

*Austropusilla* Laseron, 1954
  *Metaclathurella* Shuto, 1983
  Mem. Fac. Sci. Kyushu Univ., ser.D (Geol.) 25(1): 15
  *Austropusilla (Metaclathurella) crockerensis* Shuto, 1983

*Paraspirotropis* Sysoev & Kantor, 1984
  Zoologicheskij Zhurnal 63(7): 1096–1097
  *Pleurotomella simplicissima* Dall, 1907

*Teleochilus* Harris, 1897

*Toxicochlespira* Sysoev & Kantor, 1990
  Apex 5(1–2): 2–3
  *Toxicochlespira pagoda* Sysoev & Kantor, 1990

*Typhlodaphne* Powell, 1951

CONOIDEA INCERTAE SEDIS

*Cretaspira* Kuroda & Oyama in Kuroda, Habe & Oyama, 1971
  The sea shells of Sagami Bay: 219
  *Cretaspira cretacea* Kuroda & Oyama in Kuroda, Habe &
  Oyama, 1971

*Graciliclava* Shuto, 1983
  Mem. Fac. Sci. Kyushu Univ., ser.D (Geol.) 25(1): 11
  *Graciliclava mackayensis* Shuto, 1983

*Inkinga* Kilburn, 1988
  Ann. Natal Mus. 29(1): 230
  *Pleurotoma (Clionella) platystoma* Smith, 1877

*Kurodadrillia* Azuma, 1975
  Venus 33(4): 159
  *Kurodadrillia habui* Azuma, 1975

*Lioglyphostomella* Shuto, 1970
  Venus 28(4): 165–166
  *Drillia timorensis* Schepman, 1913

*Meggittia* Ray, 1977
  Contribution to the knowledge of the molluscan fauna of
  Maungmagan, Lower Burma...: 66–67
  *Meggittia maungmagana* Ray, 1977

*Thatcheriasyrinx* Powell, 1969

Indo-Pacific Moll. 2(10): 405

*Ancistrosyrinx orientis* Melvill, 1904 (by monotypy)

*Viridoturris* Powell, 1964 (formerly Turrinae)

## Taxa transferred to other families

*Bathyclionella* Kobelt, 1905 — Buccinidae (as synonym of *Belomitra*; Bouchet, Waren, 1980, J. Moll.Stud., suppl.8)

*Belomitra* Fischer, 1882 — Buccinidae

*Steironepion* Pilsbry & Lowe, 1932 — Columbellidae

*Surculina* Dall, 1908 — Turbinellidae (Rehder, 1967, Pacific Sci. 21(2): 182–187)

*Turrijaumelia* Sarasua, 1975
Poeyana 140: 12–13
*Turrijaumelia jaumei* Sarasua, 1975
Transferred to Columbellidae as a synonym of *Steironepion* Pilsbry & Lowe, 1932 (Finlay, 1984, Nautilus 99(2–3): 73–75)

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life history similarities among other hastulas of similar proboscis type. *Pacific Science* 33: 289–306.

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